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THE FEEDING OF NESTLING BIRDS *

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As a basis for the discussion which will follow I wish to inquire into the validity of field study as a method of developing our knowledge of bird-life. In a broad sense, by the term "field study" we mean the study of the living animal in its native habitat, under normal conditions; or under abnormal conditions which are known and determined.

It seems to me that it must be accepted as axiomatic that we have no other method of approach to certain problems of behavior. Even if this is true, however, it does not follow that the results obtained by such method are any the less subject to scrutiny and criticism. We must demand of the field zoologist the same accuracy of observation, the same careful exclusion of uncertainties, and the same rigid logic that we require of the worker in the laboratory. The observational and experimental methods are open to the one who will attempt to solve the problems of nature in the field. The laboratory worker relies upon the same methods.

I would contend, therefore, that the reliability of field studies stands in direct ratio to the scientific spirit of the investigator. The value of a report based upon field studies cannot be judged apart from the personal equation; and is this not true of every kind of investigation? Do we not require that research carried out in the laboratory be subject to verification? And is not the knowledge derived in the field by the process of observation or experimentation also open to verification?

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The successful pursuit of scientific knowledge depends upon the investigator's ability to observe and interpret; which, in turn, is largely a matter of training. Whether the observer sees through the lens of a microscope, the field glass, or with the naked eye, matters little. He is just as liable to err by the one as by the other, unless he is trained to recognize the avenues of error. Various technical equipment may be called to the aid of the observer, but, fundamentally, credibility is determined by the student's capability and honesty.

A given method of study must be appropriately used, and its limitations recognized. The microscope is to enlarge an object which is too small for direct observation. The field glass, in effect, is to bring the object closer. Both are for the purpose of rendering vision more distinct. It seems, therefore, that the field glass is as legitimate an instrument for research as the microscope. Its usefulness, however, is in the field. The extent to which it may be applied is a detail. In the identification of birds its use may be legitimate when the species possesses marks by which the identification may be thus determined. When specific differentiation is based upon minor variations in dimensions, the field glass becomes inadequate, and it must be so recognized. On the other hand, is there not also a danger that the taxonomist may go too far with his millimeter rule in the differentiation of species and subspecies?

It may be admissible to again raise the question whether, in the long run, science is advanced by the excessive multiplication of named forms which are based upon such minute structural details that the methods at the disposal of the field student become inadequate.

The tendency toward species "splitting" under the technical term of "revision" does not seem to be waning, and its bearing upon the field zoologist is so pertinent that the mention here may not be out of place.

Those ornithologists who are interested in the subject from the practical, or economic standpoint are concerned chiefly with the various problems which grow out of the question of the food of different species. Usually, the end in view, from this standpoint, is to determine the relation of birds, and of any given species, to man and to other animals in which man is economically concerned. While all of this has also a scientific value, yet the horizon taken in from the viewpoint of pure science has a vastly wider field than that which is involved in an economic study.

Without attempting to scan the entire horizon we may at once select the limited field into which we now wish to inquire. One of the subjects which has received a relatively small amount of attention is concerning the behavior of birds, and its interpretation; and particularly the behavior of birds during the breeding period, about which there is so much to learn. It is true that within recent years much more attention is being given to this phase of ornithology; but notwithstanding a rapidly growing literature along this line, on many of the problems there is not yet sufficient knowledge to enable us to safely generalize.

While other causes may have played a part in the slow development of our knowledge of the behavior of birds, it seems not unlikely that it is to be attributed, at least in part, to some prejudice against the reliability of field observations.

There are some problems which may be checked by laboratory technic, and in such cases our knowledge cannot be complete until such a check is applied. But there are some questions, which from their nature, can only be studied in the field (with respect to many species, at least). For example, there are many matters of detail about the mating of the sexes, the building of the nest, and the care of the young, etc., which cannot well be examined in the laboratory.

So when we consider the question of the feeding of nestling birds it seems that our most important method of study, and perhaps the only method in some cases, is to watch the process in nature and record the observations.

I will now review, insofar as my study of the subject permits, the facts which have been ascertained concerning the manner in which young birds are fed.

A considerable number of birds, among which, of course, are the *Limicolae,* are precocious, and forage for themselves from the beginning. Smith's paper on the Spotted Sandpiper (1)[1] reported the feeding behavior of sandpiper chicks for as early a period as I know of.

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[1] Numbers in parenthesis refer to bibliography, and page citations will sometimes be given also.

In this instance the young, which hatched during the night, were under observation from daylight of the morning of hatching, and the parents were not observed to carry any food to the young. On the other hand the young left the nest within five or six hours to feed for themselves.

If we now direct our attention to those birds which feed their young for a period of time we find considerable range of behavior. As a preliminary analysis of the subject we may distinguish three modes of feeding the young, viz.;

(a) Where the young bird thrusts its bill, or entire head, into the mouth or throat of the parent; or where the parent regurgitates the food, in a more or less digested condition, upon the ground, to be picked up by the young bird.

(b) Where there is insertion of neither bill, but a peculiar intercrossing of bills to be described in detail further on.

(c) Where the parent inserts its bill into the mouth or throat of the young in the delivery of food.

We may consider these methods in order. Perhaps the best example of the first method is furnished by the Pelican. From Chapman's admirable account of the feeding of young Brown Pelicans (2, p. 97) we learn that the naked young a day or two old takes its quota of pre-digested food from the front part of the pouch of the parent's bill, into which it has been regurgitated. Later, however, the nestling reaches far into the throat or gullet of the parent, thus exhibiting what may be called a feeding initiative.

In general this seems to be the usual method for all of the *Steganopodes*, unless there should be an exception in the Phaëthontidae. Chapman has observed the same method of feeding in the Booby (*Sulidae*), the Water Turkey (*Anhingidae*), and the Man-o-war-bird (*Fregatidae*). The Cormorants are also known to feed in the same way (2, p. 217). The same writer regrets not being acquainted with the feeding habits of the Tropic Birds (*Phaethontidae*) so that an inclusive statement might be made for the order. It is therefore unfortunate that Gross, in his most careful study of the Yellow-billed Tropic Bird (3), was not more explicit on this point. He dismisses the subject with the remark that " The food is transferred from the pouch-like gullet of the adult to that of the young by a process of regurgitation. This transfer of food is accompanied by a series of gulps, strains and wrigglings of the head and neck on the part of both birds." (3, p. 67). Attention will be called later to this description of the regurgitative process.

The Glossy Ibis, which belongs to the *Herodiones*, practices the same method. Baynard (4, p. 109) says: "The manner of the Glossy Ibis in feeding [its young] is to regurgitate the food up into the throat or mouth and for the young to put his bill, and many times his head, down the old one's throat and take his portion." As the young of this species grew older the parent would disgorge partially digested moccasins into the nest, and the young would pick up the food.

Very slightly differing from this is the account by Ward of the feeding of the young of the Herring Gull (5). Ward (quoted by Strong, 6, p. 37) describes the process as follows: "The young comes in front of an adult and with a bowing and courtesying movement puts up its bill to that of the old one, continuing the bowing for several minutes, resting between times. Sometimes it took hold of the adult's bill with its own, at other times merely touched bills. When the adult opened its mouth the young put its bill within. Failing to get indications of food, it went to another adult, and repeated the operation, passing in succession to several, until at length it seemed to get some favorable signs, for it remained by this one, alternately begging and resting. After some time it was apparent to me that the adult was striving to regurgitate. It would open its mouth, stretch nearly horizontally, then bring its head down to the ground. After a moment it would close its bill, turn its head to one side and look at the ground over which it had been straining, as though expecting to find something there. Other gulls were from time to time attracted to the scene, but were promptly chased away by this bird, who ran rapidly at them with open beak and outstretched wings. Perhaps half an hour after these efforts began I saw a portion of a fish appear in its mouth, and a moment later it was deposited on the ground, when the young promptly seized it . . . The adult assisted in breaking it up . . . The young fed mostly from the ground, but occasionally snatched a piece from the bill of the adult." Strong has made similar observations on this process in the same species (6 and 7).

In the second mode of nestling feeding which we arbitrarily recognize, the transfer of food is accomplished by the intercrossing of bills of the young and the adult, without the insertion of either. We find this method represented in at least three orders, viz., the *Tubinares*, the *Herodiones*, and the *Odontoglossae*.

In the case of the Laysan Albatross the bill of the young is placed crosswise between the mandibles of the adult. Partially digested food is then regurgitated and directed by the tongue of the adult into the open mouth of the young[2].

Among the *Herodiones* a somewhat similar method is found. Chapman (2, p. 121) has described the feeding process in Ward's Heron, the Florida Great Blue Heron, in the following words: "As the parent stepped into the nest, its bill was seized by one of the young. The young bird did not thrust its bill down the parental throat, nor was the parent's bill introduced into that of the young. The hold of the young bird was such as one would take with a pair of shears, if one were to attempt to cut off the adult's bill at the base. In this manner the old bird's head was drawn into the nest where more or less digested fish was disgorged, of which all the young at once partook."

The same author says the process of feeding the young of the American Egret is identical with that just described. Essentially the same thing is described by Gabrielson for the Bittern and the Least Bittern (8). But in these instances the food was not dropped upon the nest; it was, instead, passed directly into the young bird's mouth—perhaps a more refined and advanced process. His account for the Bittern is as follows: "As soon as she reached the nest the young commenced jumping at her beak, continuing this until one succeeded in seizing it in his beak at right angles to the base. A series of indescribable contortions followed, the head of the female being drawn jerkily in all directions and the muscles of the neck working convulsively. Finally the head and neck were placed flat on the nest for several seconds and then slowly raised again. As it [the head] came up the food came slowly up the throat into the mouth. As the food passed along the beak, the open beak of the young bird followed its course along until it slid into its mouth and was quickly swallowed. The young then released its hold and the parent stood with the muscles of the neck twitching and jerking." (8, p. 64).

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[2] I am indebted to Professor Homer R. Dill, of the University of Iowa, for the information regarding the use of the tongue by the adult albatross in feeding the young.

While the process is quite similar in the Albatrosses and Herons, one point of difference will be noted, viz., that in the former the beak of the nestling is placed crosswise between the adult mandibles, while in the latter the parent's bill is placed between the mandibles of the young.

In the Flamingo, belonging to the *Odontoglossae*, the feeding process may be referred to the same general plan, but with slight modification. The bill of the Flamingo is of such size and peculiar shape that the usual methods are not at all permissible. Neither bill is inserted in the other; nor would it be possible for the young to grasp the bill of the adult. So we find, in the words of Chapman (2, p. 187) that " What in effect is regurgitated clam broth, is taken drop by drop from the tip of the parent's bill." The food is really dropped from one bill to the other in a very dexterous fashion.

From the recent description by Gabrielson of the feeding process in the Rose-breasted Grosbeak, it might seem that there is in the *Passeres* a feeding process apparently belonging in this category (9). It would hardly be likely that this case could be related to those here described, but it is probably an adaptation of independent origin.

The third method of feeding which we will take into account consists of thrusting the food into the mouth or throat of the nestling by the parent bird. It appears to be the common method in the higher orders of birds, viz., the *Coccyges*, the *Pici*, the *Macrochires*, and the *Passeres*.

Perhaps the best analysis of this process has been given by Herrick (10) concerning the Black-billed Cuckoo. Food, which usually consists of insects, is placed by the parent well into the mouth or throat of the nestling. This act is a stimulus to the nervous mechanism of the young, and the response is a purely reflex act which sets in motion the pharyngeal muscles, thus accomplishing the deglutition of the food. The reflex act of swallowing is an automatic consequence of the contact stimulus on the throat or mouth. " This complex performance " says Herrick, " which represents the simplest sign language of the hungry bird, appears as a uniform chain-reflex, and is as predictable, and seems as mechanical as the response of the electric bell."

He points out, however, that this reflex does not long remain unmodified; that it may be inhibited by satiety, or accelerated by hunger. The rapidity of the reflex is dependent chiefly upon the hunger state; though it appears, in some cases, at least, to be necessary that the food be placed in contact with a certain region of the buccal cavity in order to provoke a prompt response. In one brood of Cuckoos with which Herrick worked he found it habitual for the adult to place its bill just within the tip of the nestling's beak, or place the insect food across between the mandibles of the young; in such instances the response was slow, the parent and young often remaining thus interlocked and motionless for five minutes by the watch, and commonly for two minutes .On the other hand, in another nest of the same species it was customary for the parents to place the food deep in the throat of the young. And here, says Herrick, " Every trial was a reaction test, and upon failure to swallow promptly, the food was withdrawn and another nestling was tested, precisely as in vireos, thrushes, and other passerine birds."

The exact conditions under which the parent awaits the reflex, or repeats the stimulus upon the same nestling, or carries the test to another bird, is a problem which may well be further investigated.

One of the interesting questions in connection with the feeding of passerine nestlings is as to the practice of regurgitation by the parents. It is quite possible that all of the passerine families are not uniform in their method of feeding the young. It is also quite probable that much of the difference of opinion in the matter is due to lack of agreement in terminology. It is, of course, important to know whether the passerine birds are uniform in this particular form of behavior.

The first necessity is the determination of the meaning of the word "regurgitation." It would perhaps not aid in our present purpose to attempt to analyse the different senses in which the term has been used by various ornithological writers, but we may at once resort to that court of appeals, the dictionary. The Century Dictionary defines the word as meaning " To pour or cause to rush or surge back." The Standard Dictionary gives the meaning as " To throw or pour back, as from a deep or hollow space; cause to surge back, as some mammals regurgitate food already swallowed."

These definitions seem to be eminently satisfactory, and I venture to presume that they will find approval in the judgment of most ornithologists. The idea of regurgitation, then, implies the previous act of swallowing of food, with concomitant reflex muscular activity. It seems reasonable to suppose that any reversal in the direction of passage would just as certainly require muscular action. And there is plenty of evidence to show that in the lower orders where true regurgitation occurs, such muscular action is clearly present. Let me remind you of the description previously quoted from Gross of the strainings and wrigglings of the head and neck of the Yellow-billed Tropic Bird in feeding the young; and of the muscular contortions of the bittern as described by Gabrielson. The photographs accompanying Fisher's account of the Laysan Albatross (11) indicate a raising and lowering of the head during the process.

Let us then consider that regurgitation cannot be accomplished without muscular effort, involving the pharyngeal muscles.

It may be objected that the position of all passerine birds in feeding is such as to permit gravitational regurgitation; that when the stomach and crop are higher than the head, the food may run down into the buccal cavity. Bearing in mind the collapsible nature of the esophageal walls when at rest, gravitational regurgitation does not seem to be a tenable hypothesis, and is not entitled to serious consideration until substantiated with some concrete evidence.

For the Coccyges Herrick's account of the life history of the Black-billed Cuckoo (10) is very complete. He makes no explicit statement as to regurgitation but the inference is easily drawn that he did not observe it.

In the case of the *Pici* the evidence for regurgitation seems to be good. Mr. William Brewster (12, pp. 233–235) gives a very complete description of the process of feeding the nestling of the Flicker. The parent approached the nest with the mandibles shut, no food visible; when the parent's bill was thrust into the nestling's throat there was a pumping movement accompanied by corresponding twitching of the tail and hinder parts of the body, and a slighter movement of the wings. As many as four young were usually fed at each visit. Similar testimony is given by Mrs. Miller (15, p. 18), by Baskett (13, p. 110), and by Burns (14, p. 54).

Passing on to the *Macrochires* we find that a considerable number of observations have been recorded.

In 1890 Mr. Brewster (16) described very vividly the feeding of the young of Hummingbirds in the following words: "Alighting on the edge of the nest, her tail pressed firmly against its outer side in the manner of a woodpecker, her body erect, she would first look nervously around, then thrust at least three-fourths of the total length of her bill down between the upraised open mandibles of the young bird. Next she would shake her head violently as if disgorging something; then, with their bills glued tightly together, both birds would remain, for the space of several seconds, perfectly immovable save for a slight, rapid, pulsating or quivering motion of the mother's throat. The actual contact of the bills lasted once for four seconds, once for six seconds, and twice for eleven seconds, the time being taken by a stop watch." . . . " The close and prolonged contact of the bills, the shaking of the mother's head, the subsequent quivering of the mother's, and, above all, the fact that after sitting on the nest for nearly an hour, she fed the young a second time without once leaving the tree in the interim, convinced me that the method of feeding was by regurgitation."

This testimony is confirmed by Shoemaker (17), for the same species, who says: " Very soon the mother bird appeared, and after a wary approach, alighted upon the edge of the nest and thrust her bill far down the throat of the young bird. I could see her throat move as she regurgitated the food. She left her bill in the little one's throat for about six seconds."

Such direct testimony cannot well be questioned without a careful re-examination of the circumstances. It should be borne in mind, however, that the length of the bill in the *Trochilidae* is a factor which must be taken into account. Even if the food, which probably consists of insects, were held in the mouth, or buccal cavity, we might suppose that some muscular action would be necessary to force it out along the mandibular tube and into the throat of the young bird. In Mr. Brewster's account it does not add to the proof that the parent did not leave the tree between feedings; since it might easily be assumed that the tree abounded in food material, i. e., insects.

We may also take into account the recorded observations of the feeding of young of the Nighthawk (belonging to the *Caprimulgidae*) which is in the same order as the Hummingbird, viz., the *Macrochires*.

Herrick watched the Nighthawk feeding its young, and says (18, p. 134) of the mother approaching the young ones: "She is loaded with fire-flies, and as her great mouth opens you behold the wide jaws and throat brilliantly illuminated like a spacious apartment all aglow with electricity. With wings erect and full-spread the old bird approached to within fifteen inches of my hand, making an electric display at every utterance of her harsh *ke-ark*. Then standing over her young, with raised and quivering wings, she put her bill well down into his throat and pumped him full. His down-covered wings were spread and a-quiver. In this position they remained interlocked and silent for one or two minutes."

Here is a case where, notwithstanding the interlocking of the parent and young for a brief period, the feeding cannot be regarded as regurgitation because the fire-flies were plainly seen in the mouth and throat as the adult approached. The question naturally arises now, may not other cases where the interpretation of regurgitation is based upon interlocking and slight quivering, be very similar to that of the Nighthawk? I am not aware that Herrick interprets this feeding process in terms of regurgitation.

Incidentally, we may note here the clear evidence of the fact that two families, at least, of the *Macrochires* feed as do the passerine birds, viz., by the insertion of the adult bill into the mouth or throat of the young. It is well to note this because of the occasional assertion that certain of the *Macrochires*, e. g., the *Micropodidae*, feed the young by taking the nestling's bill into the parental mouth.

We may now attempt to consider some of the evidence with reference to regurgitation in the *Passeres*. Perhaps the most extensive paper upon the subject is one by Mrs. Wheelock, published in 1905 (19). While this paper gives the author's observations in greatest detail, her conclusions are best summarized in the preface of her book on "The Birds of California," in which it is stated . . . "that young of all Macrochires, woodpeckers, perching birds, cuckoos, kingfishers, most birds of prey, and many sea birds *are fed by regurgitation from the time of hatching through a period varying in extent from three* *days to four weeks, according to the species.* Furthermore, that birds eating animal flesh or *large* insects give fresh (unregurgitated) food to their young at a correspondingly earlier stage of development than do those varieties which subsist on smaller insects or seeds. Also that exclusive seed eaters are usually fed by regurgitation so long as they remain in the nest."

"Out of one hundred and eighty cases in every instance where the young were hatched in a naked or semi-naked condition they were fed in this manner for at least three days. In some instances the food was digested, wholly or in part; in others it was probably swallowed merely for convenience in carrying, and was regurgitated in an undigested condition." There seemed to be no definite relation between the duration of the period of regurgitative feeding and the length of time required for full development of the young.

Mrs. Wheelock bases her paper in *The Auk* upon records of one hundred and eighty-seven broods (not species), in all of which the observations began on the day of hatching. The following families are represented in her records: *Fringillidae, Turdidae, Mimidae, Icteridae, Sittidae, Hirundinidae, Vireonidae,* etc.

Her method consisted in watching the nest at distances varying from ten to forty feet, though in some cases the distance may have been shorter; and in sampling the contents of the crop, immediately after feeding, by the insertion of a feather, and withdrawing such matter as adhered to it.

An adequate review of this important paper would be out of place in the present connection. The writer believes that the conclusions stated in the paper must be substantiated by repeated observations, since certain subsequent study has not been wholly confirmative.

As was suggested in Mrs. Wheelock's paper more notes have been published with reference to regurgitation in seed-eating birds. Thus, Wood (21) recently makes the statement that regurgitation occurs in the Goldfinch, although the evidence is somewhat circumstantial. Bergtold (22), in a very comprehensive and exhaustive account of the life-history and behavior of the House Finch, states that in that species the young are fed by regurgitation until they leave the nest (22, p. 59). A detailed description of the act of regurgitation is omitted, so that we are unable to judge what the author's conception of the regurgitative process is.

Miss Stanwood (23) incidentally states that the Olive-backed Thrush feeds by regurgitation. McAtee (24) states that Grosbeaks have been observed to feed the young by regurgitation; the same author elsewhere (25, p. 421; and 26, p. 342) takes very positive ground in favor of regurgitation, especially in the *Fringillidae*, but without offering any evidence.

We may now consider the negative testimony. Jones (27, p. 42) states that regurgitative feeding is never practiced by the Common Tern (*Sterna hirundo*).

Judd, in a very excellent account of the food of nestling birds (28, p. 412), while not explicitly discussing regurgitation, says that the first meal of the nestlings of the crow blackbird often consists of plump spiders of soft texture. Likewise, on page 425, the same author says that the first meal of the Crow usually is a young grasshopper, a plump spider, or a soft cutworm.

Jones (29, p. 69) reports the observations made by his students at the nestside of the Field Sparrow, the Song Sparrow, and the House Wren. He says: " There was no evidence that any of these birds fed by regurgitation. In the case of the sparrows this was clearly proved, but what might have happened in the case of the wrens can only be surmised. At any rate, the food was uniformly brought dangling from the bill and was not swallowed before being delivered to the nestlings. This was the case with the first feedings of both the Song Sparrows and the House Wrens."

Bigglestone (30) made a careful study of the nest life of the Yellow Warbler. All of the young were under observation within a few hours after hatching; but the last egg was under observation during hatching, and from that time onward the young bird was under constant observation till it left the nest. No regurgitation was observed, although this was one of the chief objects of the entire study.

A similar study was made of the Catbird by Gabrielson (31), in which two of the nestlings were under observation from the moment of hatching onward. Here also nothing suggestive of regurgitative feeding occurred.

During the summer of 1914 two similar nest studies were completed. The first, which has not yet been published, was undertaken by Mr. Jay Kempkes, who worked with the Western Meadow Lark (*Sturnella neglecta*) at the Iowa Lakeside Laboratory, on Lake Okoboji. Here also the results were negative, for no regurgitation was observed, although the birds were constantly under observation while in the nest; and in this instance one of the eggs was watched through the hatching process.

The second of these studies deals with the Rose-breasted Grosbeak (*Zamelodia ludoviciana*), and was carried on by Mr. Gabrielson at Marshalltown, Iowa. This report was published in a recent number of the *Wilson Bulletin* (9). The question of regurgitation was made the chief object in this study, because of the statement in one of the bulletins of the Biological Survey of the Government (24, p. 75) that the Grosbeaks feed their young in this way. The result of this very critical field study of the Rose-breasted Grosbeak was negative so far as regurgitative feeding was concerned.

While, doubtless, this review falls short of covering all of the literature on the subject, it may be sufficient to indicate that comparatively few studies have been undertaken on the passerine birds having expressly in view the question of regurgitative feeding. The writer believes the evidence is against this method in the passerine group. There seems to be a field here for much interesting and valuable work.

The question will arise, What are to be the criteria in such a problem? The scientific attitude of mind is, no doubt, the first essential qualification on the part of the observer. It is perhaps no more important in any kind of ornithological inquiry than in this close and precise field work. Certain conditions must be observed. Among other things observation at close range is essential; and close range in this connection should mean two to four feet, with the nest not above the level of the observer's eye. The study should begin, preferably, with the hatching of the egg. Definite observation must be made as to whether, or not, the food is carried visibly in the parent bird's beak. It is true that McAtee (26, p. 342) claims that the visibility of the food, held in the mandibles of the bird as it visits the young for feeding, is no disproof of regurgitation. But as we have reviewed the numerous instances where unquestioned regurgitation occurs, we have not found it customary for such species to carry food in the mandibles. And in such a proper restriction of the term "regurgitation" as I have made in this paper, and as I believe the majority of ornithologists have been accustomed to use the term, it seems to me very improbable that birds which practice regurgitation would alternate with solid food. Food apparent in the bill may not disprove that the mouth is full likewise, and that the surfeit may extend well into the gullet; but that the removal of this surfeit from the throat or gullet is to be interpreted as regurgitation is quite beyond the limits of good terminology. I believe, therefore, that food visible in the bill is very good evidence against regurgitation.

One other point to be taken into account is the presence or absence of action of the pharyngeal muscles. While this may often be a little obscure and uncertain, especially for inexperienced observers, it nevertheless may be regarded as important circumstantial evidence. If muscular activity is clearly present a presumption is established in favor of regurgitation; but if no muscular activity can be determined such a presumption cannot be claimed, to say the least.

In conclusion I may be permitted to suggest that we may, in the future, find that there is greater significance in the comparative study of the manner in which nestlings are fed than has hitherto been recognized. Among the lower orders of birds we find a method of feeding the young which we will have little difficulty in regarding as primitive. In the higher birds, such as the Passeres, we find developed a distinctly complex performance. Between the primitive and complex processes alluded to, we find feeding methods which may be regarded as transition stages. Without, at this time, attempting a too rigid arrangement of these feeding processes, as to their natural and phylogenetic sequence, we may at least be justified in the conclusion that the problem deserves much further study. Whether any importance might be attached to such a quasi-physiological process in the determination of affinities it would be premature to speculate. But that this may be no more than a random suggestion, only future investigation can determine.

REFERENCES

(Arranged in order of citation)

1. Smith, Arthur F. Notes on the Spotted Sandpiper. *Wils. Bull.*, XXVI, 1914, pp. 81–86.
2. Chapman, Frank M. Camps and Cruises of an Ornithologist. New York, 1908.
3. Gross, Alfred O. Observations on the Yellow-billed Tropic Bird (*Phaethon americanus* Grant) at the Bermuda Islands. *Auk*, XXIX, 1912, pp. 49–71.
4. Baynard, Oscar E. Home Life of the Glossy Ibis (*Plegadis autumnalis* Linn). *Wils. Bull.*, XXV, 1913, pp. 103–117.
5. Ward, H. L. Notes on the Herring Gull and the Caspian Tern. *Bull. Wisc. Nat. Hist. Soc.*, IV, 1906, pp. 113–134.
6. Strong, R. M. On the Habits and Behavior of the Herring Gull, *Larus argentatus* Pont. *Auk*, XXXI, 1914, pp. 22–49, pp. 179–199.
7. Strong, R. M. On the Habits and Behavior of the Herring Gull, *Larus argentatus* Pont. *Report Smith. Inst.*, 1914, pp. 479–509.
8. Gabrielson, Ira N. Ten Days' Bird Study in a Nebraska Swamp. *Wils. Bull.*, XXVI, 1914, pp. 51–68.
9. Gabrielson, Ira N. Field Observations on the Rose-breasted Grosbeak. *Wils. Bull.*, XXVII, 1915, pp. 357–368.
10. Herrick, Francis H. Life and Behavior of the Cuckoo. *Jr. Exp. Zool.*, IX, 1910, pp. 169–233.
11. Fisher, Walter K. On the Habits of the Laysan Albatross. *Auk*, XXI, 1904, pp. 8–20.
12. Brewster, William. A Brood of Young Flickers (*Colaptes auratus*) and How They Were Fed. *Auk*, X, 1893, pp. 231–236.
13 Baskett, J. N. . . . *Nidologist*, II, p. 110.
14. Burns, Frank L. A Monograph of the Flicker (*Colaptes auratus*). *Wils. Bull.*, XII, 1900, pp. 1–83.
15. Miller, Olive Thorne. First Book of Birds.
16. Brewster, William. Food of Young Hummingbirds. *Auk*, VII, 1890, pp. 206–207.
17. Shoemaker, Frank H. A Late Nest of the Ruby-throated Hummingbird. *Proc. Nebr. Ornith. Union*, II, 1901, pp. 34–38.
18. Herrick, F. H. The Home Life of Wild Birds. New York, 1905.
19. Wheelock, Irene G. Regurgitative Feeding of Nestlings. *Auk*, XXII, 1905, pp. 54–71.
20. Wheelock, Irene G. The Birds of California.
21. Wood, J. Claire. The Food of Nestling Goldfinches. *Wils. Bull.*, XXV, 1913, p. 96.
22. Bergtold, W. H. A Study of the Finch. *Auk*, XXX, 1913, pp. 40–73.
23. Stanwood, Cordelia J. The Olive-backed Thrush (*Hylocichla ustulata swainsoni*) at His Summer Home. *Wils. Bull.*, XXV, 1913, pp. 118–137.
24. McAtee, W. L. Food Habits of the Grosbeaks. Bull. 32, *U. S. Bur. Biol. Survey*, 1908.
25. McAtee, W. L. Field Studies on the Food of Nestling Birds. (A review). *Auk*, XXXI, 1914, pp. 420–421.
26. McAtee, W. L. Correspondence. *Wils. Bull.*, XXVII, 1915, pp. 339–344.
27. Jones, Lynds. A Contribution to the Life History of the Common (*Sterna hirundo*) and Roseate (*S. dougalli*) Terns. *Wils. Bull.*, XVIII, 1906, pp. 35–47.
28. Judd, Sylvester D. The Food of Nestling Birds. Yearbook, *U. S. Dep't. Agric.*, 1900, pp. 411–436.
29. Jones, Lynds. Some Records of the Feeding of Nestlings. *Wils. Bull.*, XXV, 1913, pp. 67–71.
30. Bigglestone, Harry C. A Study of the Nesting Behavior of the Yellow Warbler (*Dendroica ae. aestiva*). *Wils. Bull.*, XXV, 1913, pp. 49–67.
31. Gabrielson, Ira N. Nest Life of the Catbird. *Wils. Bull.*, XXV, 1913, pp. 166–187.

Sioux City, Iowa.

A STUDY OF THE REACTIONS OF CERTAIN BIRDS TO SOUND STIMULI

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I. INTRODUCTION

This problem was undertaken at the Biological Station of the University of Michigan, under the direction of Professor R. M. Strong, between the dates of July 10 and August 21, 1916.

The Biological Station is located on Douglas Lake, in the western part of Cheboygan County, Michigan. The region immediately about the camp is covered with a fairly dense stand of young aspens, birches, and pin cherries, with occasional oaks and maples. This is the type of vegetation which has succeeded the original forests of pines and hardwoods in this cut-over and burned-over country. A few pines remain, chiefly along the lake shore, but there are no hardwoods in the immediate vicinity of the Station. Another important type of vegetation is found in the dense cedar bogs, where "arbor vitae, balsam, tamarack, and spruce form a nearly impenetrable jungle."

The bird life naturally shows a marked ecological concentration of species in these widely different habitats. In order that observations on any species might be made as nearly continuous as was desired, it was thought best to work with nesting birds as far as possible; and accordingly on July 5 search was begun for suitable subjects. But although birds are really fairly plentiful in the aspens during the early summer, the abundance of nesting sites furnished by so extensive and so uniform a habitat as the aspen association made the discovery of nests very difficult. In fact, it was not until the morning of July 8 that a nest was found located so that work could successfully be carried on.

The nest referred to was that of a hermit thrush. It was placed on the ground in a small cluster of oak seedlings, about a hundred feet from the shore of Douglas Lake. Work was begun here on July 10, and was continued until the young birds left the nest. By far the greater part of the summer's work was done on these hermit thrushes, because the nest was easily accessible from the Station, and because the hermit thrush proved a good subject for experiments of this sort.

Another nest, that of a robin, was discovered some days later, within the limits of the camp. Although for more than two weeks efforts were made to test the auditory reactions of this bird, it was found to be too timid for practicable experiments.

In addition some work was done in connection with this problem on birds found in the field, particularly on some of the birds characteristic of the cedar bog, and with some shore birds. Experiments were also made upon some young cedar waxwings which had been taken from their nest and placed in a cage for special study; but by the time that my experiments were begun the waxwings had become so accustomed to the presence of various people and to noises of all sorts that no positive results could be obtained.

II. METHODS AND MATERIALS

The experiments with the nesting hermit thrush were for the most part made with the aid of a small white observation tent which was pitched so that the apertures for observation were within six feet of the nest; and a narrow path from these apertures to the nest was cleared of grasses, etc., so as to admit the making of photographs. The tent was first pitched on the morning of July 10, and it was taken down the same day; on July 12 it was replaced and was left standing until all the work possible on the hermit thrushes had been completed.

The observations on the birds of the cedar bog and on the other birds experimented with in the open field were made without the use of any special shelter. Great care was taken to avoid other than auditory stimulation.

The sounds used were made as varied in character as possible. Those tried on the hermit thrush included shouting, singing, whistling both with the lips and with a "double-tone" metal whistle, chirping with the lips, clapping the hands, rapping on wood and on metal, and rustling papers and birch-bark. To test the reactions to sounds of different pitch a mandolin was used. The same sounds were also used in the case of the other birds, but such as involved sudden movement, as clapping the hands or rapping on wood or on metal, were not tried to any considerable extent. There is a possibility that auditory stimuli may sometimes have been accompanied by visual stimuli in the case of the thrushes when the giving of the sound required motion on my part. My blind was pitched between the nest and the morning sun, and the tent-walls were very thin, so that movements within it were often perceived vaguely from the outside.

The reactions to all these stimuli were more or less similar, differing in degree only. In every case they consisted of movements of the head and of the bill, of raising the wings, and of winking. The eye-wink, however, is of doubtful value, and was considered only in the case of the thrushes. The interval between the giving of the stimulus and the perception of the reaction to it seemed fairly constant for those birds which reacted at all, being about three-fourths of a second, as nearly as could be determined.

III. OBSERVATIONS

1. On the nesting hermit thrush. July 10, 9:10–10:50 a. m., 1:30–3:20 p. m. The bird was not much alarmed, even at the very first, by my stirring about in the tent, but flew when, at 9:20, I caused the side of the tent toward the nest to flutter. It returned in two minutes, and took its usual position on the nest, facing the tent obliquely, with its head turned toward the woods, to which the bird always went on leaving the nest, rather than toward the lake. Only rarely, and then usually in response to sound stimuli, did it turn its head directly toward the tent. I never saw it approach the nest except from the side *toward* the blind.

The first time that I released the shutter of my camera the bird showed decided alarm, but this was of short duration, less than three seconds. Rapping with a pencil on the metal cover of my note-book caused the bird to turn its head from side to side, as if it were trying to locate the source of the sound. A short blast on the whistle caused the same reaction, apparently of about the same intensity; when this experiment was repeated the same result was obtained, but after the tenth trial the bird seemed to have become accustomed to it, and the only response it made was merely to assume a more alert attitude.[1]

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[1] Similar observations were made by Strong on gulls studied from a blind. Strong, R. M., 1914. On the Habits and Behavior of the Herring Gull, *Larus argentatus* Pont. *The Auk,* vol. 31, Nos. 1–2, pp. 22–49, 178–199; plates 1–10, 19, 20, also *Smithsonian Report,* 1915, pp. 479-509.

Even so faint a sound as that made by my pencil in writing on the note-book page seemed to cause the bird some uneasiness. Singing caused very slight apprehension, not nearly so much as did the sound of the waves thrown up on the shore by a passing launch. At the second release of the camera shutter the bird showed less concern than was evident the first time; but when I moved the camera in winding the film, it was alarmed to the point of standing in the nest, and it even walked off while I was rewinding the shutter curtain. It was gone only five seconds.

In the afternoon a companion accompanied me when I returned to the blind. The bird stayed on the nest when we entered the tent; but when I moved my finger in the aperture it showed great alarm, and left the nest when I flashed a mirror there: it was gone seventeen minutes. On its return I waited for several minutes before attempting any experiments. I noted that the bird was always on the alert, particularly for sounds from the tent; however, it was not insensible to other sounds, for several times it took food, usually large ants, from the edge of the nest, apparently in response both to auditory and to visual stimuli; the thrush seemed to be made aware of the ant through an auditory stimulus, and then to discover it through the visual sense. The bird seemed also to start visibly at sudden noises from outside the tent; but on this date it was concerned chiefly with those which were made within the blind.

The day was clear and warm, and the bird panted considerably. I found that usually it would close its bill when I made a sudden sound, and would turn its head and wink its eye, while to sounds from outside the tent the response consisted usually in merely turning the head. The bird sometimes turned its head at our conversation, but usually it paid no attention to it; once it seemed quite disturbed at the noise made by tearing birch-bark. My companion left after half an hour in the tent.

The slightest movement of the tent-wall near any of the apertures was sufficient to attract the bird's attention, but it seemed only slightly concerned by the movements of the canvas elsewhere. A sudden gust of wind sounding in the pines overhead caused the bird to start slightly, and soon afterward it started noticeably at a junco's song from the same trees. Then, later, when I tapped on my note-book cover with my pencil, the bird looked about over its head as if trying to discover the source of the sound.

During the afternoon I tried the effect of song on the bird, but I obtained no positive results. I did notice, though, that if the song were suddenly broken off and two or three sharp raps given on the tent pole, the bird reacted more vigorously than to the raps alone. And a suddenly *ended* loud sound seemed to startle it more than a sudden loud sound did ordinarily. These reactions were noticed several times during the afternoon, but they became much less marked on successive repetitions of the experiment.

July 12, 9:25–10:40 a. m., 1:10–3 p. m. The bird seemed very uneasy at noises made outside the tent, particularly at the loud cawing of some crows. After about half an hour of quiet, I blew a loud blast on the whistle, which produced only a slight reaction. The squeaking sound made by kissing the back of the hand vigorously produced no visible reaction. The higher pitched of the two whistle notes, when sounded alone, seemed to produce a slightly more vigorous reaction than did the lower one alone. But no whistle blast produced so strong a reaction as did the sudden loud call of a cuckoo from the near-by aspens.

The visual stimulus produced by a moving object seemed very much stronger than did any auditory stimulus; when I showed my fingers at the aperture the bird showed very decided alarm. As the experiment was repeated the reactions became much less pronounced.

In the afternoon I took a mandolin to the tent; and, as with the whistle, the notes of higher pitch seemed to produce slightly more vigorous reactions. However, the differences in the reactions were so slight that it was very difficult to make such determinations. The notes used ranged over about two octaves, from the open G-string of the mandolin to B two octaves higher.

I found that a chord produced a more vigorous reaction than did any single note; however, the bird quickly became accustomed to the chord, and after half a dozen trials merely showed increased vigilance. As on July 10, I found that if a sound was interrupted by another of very different character, a more vigorous reaction was produced than by mere suddenness or loudness of sound. After the bird had become accustomed to the mandolin and to the whistle so as to react to them only slightly, I tried the effect of interrupting the mandolin chords by loud whistle blasts, and found that the bird reacted markedly, though with decreasing vigor as the experiment was repeated.

I experimented also on the combination of auditory with moving visual stimuli. As stated above, the sudden appearance of my finger at the aperture seemed to startle the bird, but the reaction decreased rapidly in vigor on successive trials. The same was true of the reaction produced by sounding the open G-string of the mandolin. If, however, I showed my finger at the aperture, then, after a short pause, moved it suddenly and at the same instant sounded the G-string loudly, the bird reacted vigorously; and *the reaction was as strong at the thirtieth trial as at the first.*

July 13, 8:45–10:20 a. m., 1:10–3:20 p. m. The work in the morning was similar to that of the two days previous, and the reactions observed were similar, though less vigorous on the whole. The combination of auditory and visual stimuli was tried again, and the same results were obtained by combining the movement of my finger with a loud whistle blast as with a mandolin sound; although fifteen trials were made, there was little, if any, diminution in the vigor of the reaction, which in this case consisted usually in turning the head and closing the bill momentarily.

In the afternoon I approached the nest from the side opposite the tent. I crept up over a thick growth of bear-berries without taking particular pains to move quietly, so that I am sure that the bird must have heard me. The bear-berries screened me from the nest, so that until I came within three feet of it I could not see the brooding bird. I found that the bird seemed not at all on the alert for any disturbing sound from the tent, nor had it seemed to notice my approach. I then blew a loud blast on the whistle, but it showed no sign of fright, and merely turned its head slowly until it caught sight of me, when it immediately left the nest.

I then concealed my watch carefully about six inches from the nest, and immediately entered my tent. When, after fifteen minutes, the bird returned, it was very plainly made uneasy by the ticking of the watch; it turned its head from side to side, and looked for it when once its approximate location had been determined from the sound. After about half a minute, however, the bird gave up the search and paid no more attention to the watch.

The bird now seemed constantly on the alert for sounds from the tent, having seen me enter it; very slight reactions were noticed, however, to whistling, shouting, and clapping the hands, while rapping on wood and chirping with the lips produced no visible reactions.

July 16. The three eggs hatched this afternoon. I made no observations.

July 17, 8:40–9:30 a. m., 1:10–3:10 p. m. There was no sign of either parent during the fifty minutes I spent in the tent in the morning. In the afternoon one of the parents was at the nest when I approached, and stayed while I entered the tent. On this date, for the first time, I obtained a response to the chirping sound. To it the bird responded by turning the head, often as much as 90 degrees, and by winking. Although the interval between winks varied between such wide limits as two seconds and thirteen seconds, I think that the wink can safely be considered as a part of the reaction, since in each case it accompanied the turning of the head, about three-fourths of a second after the sound stimulus was given.

To the higher-pitched of the two whistle notes the bird again reacted slightly more vigorously than to the lower; the reaction here consisted in turning the head and closing the bill. The reaction to this sound was on this date much less vigorous than that to the chirping.

I tried a new vocal sound successfully; a rapid, rolling "rr-r-r-rr." To this the bird responded on six out of seven trials, showing alarm not merely at the beginning of the sound, but as long as it was continued.

The experiment of changing from one sound to another of a different sort gave results this day on only three trials out of seven. However, the bird seemed more responsive to all other tests than on the last day that observations were made before the hatching of the eggs.

July 19, 9–10:40 a. m. The young birds' eyes were just opening when I began my observations. Any small sound from the tent seemed to stimulate the nestlings to raise their heads as if for food; and I noticed that in this connection such sounds as rustling paper or birch-bark were stronger stimuli than were sharper sounds such as tapping or chirping. When the parent returned it stood in the nest over the young, and was continually on the alert. The usual sound stimuli were tried—tapping, whistling, clapping the hands, etc.—and the usual reactions were secured. Interrupting a sound by another of a different sort produced vigorous reactions twice in three trials. For the first time since July 10 the bird seemed to be made uneasy by the sound of my pencil; when I started writing it gave a slight reaction, and again when I stopped writing. This was the first day since July 10, however, when the wind was blowing from the tent toward the nest.

When I made my first photographic exposure this morning, the parent on the nest had ceased momentarily to watch the tent and was bending over the young. The sound of the camera aroused it to watchfulness again. Subsequent releases of the camera shutter did not seem to attract the bird's attention at all.

July 20, 9:10–10:50 a. m. While the parent was absent I tried the effect of a loud whistle blast on the nestlings. At the first trial one of them raised its head, but five subsequent trials produced no effect.

When a parent returned I made some experiments to determine to what extent reactions were inhibited when the bird was at the nest. While it was approaching the nest and when within a few inches of it, I tried various sounds, but without effect. When this bird had finished feeding the nestlings, I gave a loud whistle blast, and the bird started visibly. Later, when a parent approached the nest again, and was still five or six feet away, I tapped my note-book cover with my pencil, with the result that the bird turned and ran off some fifty feet. When it returned a minute later I repeated this experiment, and the bird flew away and was gone several minutes. After several feedings I made some further experiments, with the following results: when the parent was coming to the nest and was within a few inches of it, or when at the nest-side and engaged in feeding the nestlings, it seemed to pay little or no attention to sounds from the tent; but after the young were fed and the nest was cleaned, it seemed always to notice them. Yet it was by no means as responsive (on this date) to any sounds from the tent as to the very faint lisping sounds with which the young asked for food.

July 21, 8:30–10:45 a. m., 1:20–2:30 p. m. One of the nestlings was lying in the nest, when I entered the tent, with its head raised and bill opened so that the lower mandible lay on the edge of the nest. I clapped my hands several times at considerable intervals, and each time the young bird responded by raising its head nearly to a vertical position and closing the bill slightly. When a parent returned I repeated the experiments of the day before, and again I found that the reactions were greatly inhibited when the bird was at or near the nest, and that the bird when at the nest seemed to pay much more attention to the sounds made by the young than to any sounds I made. In the afternoon I repeated experiments on the nestlings, but the only response obtained was similar to the one just described.

July 24, 8:05–11 a. m. During the first fifteen minutes of the period the young were very quiet. I observed that whenever I made any sudden loud noise, one of the nestlings invariably raised its head, opened its eyes, and (apparently) watched the tent for a few seconds. If the sound were repeated, it did not show any further alarm, but merely continued to watch the tent for a somewhat longer period than if the sound were not repeated. I also noticed that the nestlings never seemed to be aware of the approach of the parent, whether it ran or flew to the nest-side; and it was my experience that its flight was very noisy, with loud whirring of the wings, when it approached the nest. In direct contrast to this was the case of some cedar waxwings which came to my attention during the summer; here the nestlings seemed always to be aware of the parent's approach at a distance, and for some time were in a state of expectancy.

Except in the cases mentioned in the preceding paragraphs I was never able to obtain any marked response from the nestlings to sudden and loud sounds. This seems to me to be directly contradictory to a statement of Lloyd Morgan (Animal Behavior, p. 49) to the effect that young birds "show signs of alarm at any sudden and unaccustomed sound." After I had been in the tent twenty minutes and the young birds had become entirely quiet, I repeated the experiments with various kinds of sounds, as whistling, rapping on wood and on metal, clapping my hands, etc., but I was unable to detect any positive reactions.

I also continued the observations on the inhibition of reactions in the parent when near the nest, with the same results as before.

July 25, 8:25–10:30 a. m. The observations made from the tent this morning were substantially the same as those of the day before, except that for the first time I was sure that both parents came under my observation. I was not able to detect any difference in their behavior.

At 9:45 I left the blind and withdrew for about ten minutes. On my return I waited until a parent had finished feeding the nestlings and had left the nest, and then, instead of going to the blind at once, I took advantage of some natural cover to conceal myself. Neither of the parent thrushes seemed to pay the slightest attention to me on their subsequent visits to the nest, nor did either of them respond visibly to any sound that I made, though I tried shouting, whistling, and chirping loudly. But after I reentered the tent (at 10:15) I found that both birds reacted markedly to these same sound stimuli.

2. Observations on a young hermit thrush. In the late afternoon of July 26 a young thrush was taken from this nest for the purpose of studying its reactions to sounds under laboratory conditions. On this date it gave no evidence of reactions to sounds or of the formation of associations between sounds and other events. On the two days following there was no opportunity to study this bird.

On July 28, a very warm and sultry day, the bird became sick, due doubtless to the heat and to the change in environment and feeding; it was transferred to a more airy cage. The next day the temperature was still higher and the bird was still sick; yet it was very active, and made violent efforts to escape from the cage, with the result that it so nearly exhausted itself that it was practically unable to open its eyes. It was on this date that the first observations were made which showed any ability on the part of the bird to associate sounds with other events. For instance, after the bird had been fed four times, it was noticed that when the door of the cage was rattled the bird turned toward it at once and begged for food. If food were not forthcoming, this reaction became less and less vigorous on successive trials, and finally ceased altogether until the bird had been fed again. In the afternoon of the same day the thrush was taken outside the cage; and even under these conditions, and when at some distance from it, the bird continued to orient itself toward the source of the sound and to beg for food when the cage door was rattled. During all of these experiments the bird kept its eyes tightly closed.

Further experiments were planned, but the thrush died on July 30.

3. Observations on birds of the cedar bog. On August 13 I went down into a dense cedar bog about two miles from the station, and, while in the more open parts, I ran across a flock of chickadees, golden-crowned kinglets, and brown creepers, numbering perhaps thirty individuals. I tried the effect of whistle blasts, of clucking with the mouth, and of shouting, all at a distance of less than fifteen feet, without obtaining a positive reaction from any of these birds; nor did this surprise me, when the fearless habits of these birds were considered. When I clapped my hands, however, a kinglet did fly to a farther tree; but this was undoubtedly due rather to the effect of the visual than to the auditory stimulus. Later I tried the effect of a whistle blast on a black-throated green warbler, with more positive results. The bird raised its wings as if to fly, but soon settled back and then continued its search for food. Subsequent trials produced no result.

4. Observations on young cedar waxwings. As was stated in the introduction, these waxwings were so accustomed to sounds of all sorts before my experiments were begun that almost no positive results were obtained. In fact the only thing definitely established was that these birds were more responsive to sound stimuli before being fed than afterward.

5. Observations on certain shorebirds. On August 21, I made a series of observations on some solitary sandpipers, least sandpipers, and kildeers which were feeding on the beach near camp. I tried whistle blasts, shouts, and percussive sounds, both vocal and clapping my hands. The only reaction I observed among the sandpipers was given by a solitary sandpiper, which

raised its wings when I clapped my hands. To the whistle blasts the kildeers responded at first by running a few steps along the shore, but later they gave no reaction to this sound. To cluckings they did not respond, but when I clapped my hands the whole flock took flight. The visual stimulus undoubtedly was the stronger in bringing about this reaction.

Later I made similar experiments on a solitary kildeer, without obtaining any positive results.

IV. SUMMARY

1. The hermit thrush was constantly on the alert as long as I was in the observation tent, and while I was there it seemed very often to be more sensitive to sounds from without the tent than to those which I made inside.
2. If a continued sound were suddenly interrupted by another loud sound of a very different character, the bird reacted more vigorously in most cases than to either sound alone.
3. The hermit thrush seemed not particularly sensitive to sounds when no one was in the tent.
4. An auditory stimulus produces a much stronger reaction in birds when it is reinforced by a moving visual one, and a moving visual stimulus when it is reinforced by an auditory stimulus.
5. The hermit thrushes under observation very soon became accustomed to various sounds and in a short time ceased to react visibly to them unless the sounds were reinforced by other stimuli.
6. The hermit thrush was very much more sensitive to sound stimuli early in the period of experimentation than later, and there was a secondary maximum just after the hatching of the eggs.
7. The reactions to sounds on the part of the hermit thrush are very much inhibited when the bird is at the nest or within three feet of it, but this inhibition is much less after the young are fed than before.
8. The adult hermit thrush is apparently more sensitive to notes of higher pitch than to sounds of lower pitch.
9. Very young birds were more influenced by such sounds as the rustling of paper or of birch-bark than by sharper sounds such as tappings, whistling, etc.

10. I found the young of the hermit thrush during the first ten days after hatching very little influenced by sound stimuli.

11. A thirteen-day old hermit thrush very quickly learned to associate certain sounds with feeding.

12. Shore birds, chickadees, golden-crowned kinglets, and brown creepers observed in the field were not visibly influenced by sound stimuli. A slight response was obtained from a black-throated green warbler.

13. From a rather unsatisfactory study of young cedar waxwings it appears that they are more sensitive to sounds before being fed than afterward.

CHOICE OF FOOD IN AMEBA

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INTRODUCTION

In a previous paper ('16a) I outlined the problem of choice of food among animals as I conceive it, and in this paper I wish to discuss the power of choice in ameba as exhibited in the various series of experiments recorded in several of my previous papers, as well as in experiments which are recorded for the first time in this paper.

The problem of choice of food has turned out to be very intricate and difficult; much more so than was at first suspected. It is rendered especially difficult because previous experience in sense perception plays a very important part in selection. Choice thus becomes in large part a developing or historical process. Series of individual acts of choice are the smallest units which can be considered in analyzing this problem. Individual acts of choice are frequently quite meaningless, and even contradictory to each other, when removed from their historical setting. This fact is of the greatest importance in this connection and must not be lost sight of.

Before a discussion of choice of food is entered upon, I wish first to describe two series of experiments which have particular bearing on this matter. One series has to do with choice expressed by an ameba when encountering two particles of different composition lying very close together, while the other series deals with the effect of mechanically agitating various kinds of particles in close proximity to the ameba.

REACTIONS TO TWO PARTICLES OF DIFFERENT CONSTITUTION LYING CLOSE TOGETHER

Globulin and silicic acid.[1]—A grain of globulin and a grain of silicic acid were laid close together in the path of an Amoeba proteus[2]—figure 1. The test objects were laid some distance ahead so that all the changes in behavior due to the test substances could be observed. The ameba moved directly forward for a considerable distance, then sent out on either side several pseudopods which were, however, soon retracted—3. As the ameba moved further forward toward the test substances, it broke up into three pseudopods, the middle one of which pointed directly toward the silicic acid, though it did not move into contact with the acid—5. The right-hand pseudopod was retracted while the ameba moved on through the pseudopod on the left, gradually swinging around the silicic acid, and coming into contact with the globulin from the opposite direction. The globulin was ingested without the formation of a food cup, while the silicic acid was carried to the back of the ameba where it remained a short time.

Silicic acid and egg albumin.—The ameba whose reactions to globulin and silicic acid were described above, later reacted positively to, but finally avoided, a capillary tube containing a solution of egg albumin—14. After this test a grain of silicic acid was laid in front of the tube of albumin—26. The ameba moved toward the silicic acid until within about fifty microns of it when there were formed several side pseudopods, of which the one on the right became the main pseudopod. But this one soon curved to the left and toward the silicic acid, and then kept on moving in this direction until within thirty microns of the acid when the tip of the main pseudopod turned slightly to the right and moved past the test object—35. But as soon as the tip of the ameba was well past the silicic acid, the ameba turned toward the open end of the tube and a small pseudopod was also sent out toward the tube—38. The ameba, however, moved away from the tube of albumin through a pseudopod sent out on the right. This experiment demonstrates very clearly that, although the mere presence of a solid object immersed in a solution of some other substance serves to attract an ameba, the main factor in determining the movements of an ameba is either the increasing density of the diffusing molecules or ions as the source of diffusion is approached, or some other physical disturbance propagated radially from the source of diffusion.

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[1] For method of preparation of the test substances mentioned in this paper reference should be made to my former papers, '16b, '16c.

[2] For a description of the species of ameba mentioned in this paper refer to my paper '16d, in Science. In previous papers I spoke of 'raptorial' and 'granular' amebas. Raptorial amebas are of the species Amoeba dubia Schaeffer, while the granular amebas refer to two species: Amoeba proteus Pallas emend. Leidy, and Amoeba discoides Schaeffer. From my notes I am unable to tell in all cases to which of the latter two species the granular amebas belonged. This is due to the fact that discoides was not discovered to be distinct from proteus until after these experiments were made. In this paper therefore, the label A. proteus includes also the species discoides.

(Figures 41-50 represent a control experiment showing that silicic acid by itself does not cause a positive reaction.)

Globulin and soluble egg albumin.—In an experiment similar to the preceding, on the same ameba, but in which a grain of globulin was used instead of silicic acid—51, the ameba moved away from the tube of egg albumin after the globulin was eaten—65. This experiment, when studied in connection with the preceding experiments upon this ameba, shows very strikingly the nice discriminations in the selection of food which this animal is capable of making.

Carbon and lecithin.—The lecithin bore Merck's label and was made from eggs. A small amount of it was smeared on a carbon grain which was then laid in the path of an A. proteus—101. The ameba moved forward into contact with it, and then moved off through a pseudopod which had been forming on the left—107. The carbon-lecithin was then shifted—109. The ameba moved toward the test object, then turned toward the left, then moved forward into contact with it again, and then moved on leaving the carbon-lecithin behind. A new piece of carbon, with fresh lecithin was then placed near the ameba—115. The ameba moved forward into contact with it and then passed on. A small pseudopod was thrown out posterior to the carbon-lecithin, and later another anterior to it, but the ameba finally moved away without attempting ingestion.

Globulin and lecithin.—A grain of globulin was smeared with lecithin and placed in the same ameba's path—123. The ameba moved forward a short distance toward the test objects, then turned to the left, avoiding them.

Globulin and hematin.—A grain of hematin and a grain of globulin were laid close together in the path of an A. proteus—67. As the ameba moved forward a pseudopod was thrown out on the left toward the globulin-hematin. A food cup was formed and both substances were ingested. There was no period of rest, the ameba moving on in the same direction. The hematin remained in the ameba's body for a considerable time thereafter. A little later another grain of hematin and one of globulin were laid in the ameba's path—78. The ameba moved into contact with them and carried them up on its back—82, and then formed a food cup extending upwards and ingested them. The ameba remained comparatively quiet for a short period, then moved on in the original direction. Another grain of hematin was then laid with a grain of globulin some distance ahead of the ameba—87. The ameba moved forward toward the test objects and when within about seven microns of them—91, 92—the tip of the main pseudopod spread out and formed a food cup over them just as if they were moving organisms like flagellates. The food cup was completed and the hematin-globulin taken into the protoplasm as on the two previous occasions. The ameba quieted down for a few minutes, then moved off about thirty degrees to the left of the original direction.

No attempt was made by the ameba in any of these experiments to separate the globulin from the hematin and to ingest the globulin only, leaving the hematin behind. But it is to be noted that in all these experiments the globulin grain was much larger than the hematin. The most remarkable incident is the ingestion in a food cup—93, 94—where the food cup was formed before the ameba had come into actual physical contact with the hematin or the globulin.

Globulin and uric acid.—A large grain of globulin and a small grain of uric acid were laid close together in the path of the ameba used in the experiment with hematin and globulin recorded above—129. The ameba moved forward into contact with the globulin-uric acid and ingested them without the formation of a food cup. The ameba remained quiet for about five minutes, after which it moved off in the original direction.

Globulin and carbon.—A small grain of carbon was laid on a larger grain of globulin in the path of an active A. proteus—138. The ameba moved forward in Y-form with the carbon-globulin lying between the prongs. The right prong finally became the more active and in its forward movement dragged the retreating left prong into contact with the globulin-carbon—147. A pseudopod was then sent out against the test substances which upset them so that the carbon lay between the ameba and the globulin. A large food cup was then formed over both substances—149. The carbon grain was soon pushed out of the food cup while the globulin was taken into the protoplasm. Just how this happened could not be determined, but it was not "accidental."

Another grain of carbon together with one of globulin of about the same size, were laid in the path of an A. proteus—151. The ameba moved forward to the right of the test substances—153. A side pseudopod was then sent out to the left. It passed the carbon on the left. A small pseudopod was then sent out into contact with the globulin grain—157. A large food cup was then quickly formed over the globulin-carbon—158—but presently the carbon was pushed out while the globulin was taken into the protoplasm. The details of the separating process again could not be observed.

A grain of globulin was then placed on a large grain of carbon in the path of a large ameba belonging to the proteus species—159. As the ameba moved forward a pseudopod was thrown out on the left—160, but it was soon withdrawn—162. The main pseudopod flowed on past the carbon-globulin and then turned sharply to the right—164. A small Y-shaped pseudopod was sent out toward the test substances as the ameba moved away, but it was retracted before it had covered more than half the intervening distance—164. The grains of carbon and globulin were then shifted—165. The ameba moved past them a short distance—168. The tip of the main pseudopod then turned to the left and moved into contact with the test substances. The carbon-globulin grains which were sticking together slightly, were rolled around a few times by the ameba. A food cup was then formed with the test substances lying, not in the food cup, but in the mouth of it—172. Half a minute later another food cup was formed over them, but the ameba did not fuse the free ends of the cup until four minutes after forming it—172. The ameba then quieted down for about thirty-minutes, during which time but very little movement could be observed; nevertheless the globulin and the carbon became separated from each other, the carbon lying in the anterior half and the globulin in the posterior half—178. The ameba then moved off in the direction opposite to the original, but so that the carbon should at once occupy a position at the posterior end. A few minutes later the carbon was excreted. Ten minutes after the ameba had enclosed the carbon and the globulin in the food cup, another normal food cup was formed while the ameba was lying quiet, but there was no solid substance in it, nor was there anything in the vicinity to cause its formation. The stimulus producing it must have been internal.

This is a remarkable series of experiments. A degree of precision in food discrimination is disclosed in these observations which was altogether unsuspected. The separating process in the first two experiments is not understood. Not all the details necessary to an understanding of the process were observed. The ameba reacted like a higher animal might if reduced to ameboid form. The last experiment clearly indicates that the ameba was "aware" of the presence of a particle that was not food lying close to one that was food. The way in which the first food cup was formed clearly shows this. The long delayed fusion of the free edges of the food cup indicates the effect of the disturbing carbon. The long rest of thirty minutes also is unusual. The change in the direction of locomotion was doubtless caused by the position of the carbon. And the formation of the empty food cup during the resting period was in some way incited by the disturbing carbon, but just what connection there might be between the two remains unknown.

Gluten and glass.—In the path of an A. dubia that had just previously ingested pieces of agitated glass, was placed a piece of glass and a piece of gluten lying close together—179. The ameba moved into contact with the gluten and the glass—184-186—and then carried them up on its back, but there was no attempt to ingest either of the substances.

Globulin and Coleps hirtus.—A small mass of metallic iron was temporarily attached to a grain of globulin and slightly agitated with an electric coil. The Amoeba dubia near which the globulin lay, nevertheless treated it with indifference. A coleps then came along, and while hovering over the globulin, both the globulin and the coleps were ingested by the ameba in a food cup thrown out from the posterior end—190. Five minutes after the formation of the food cup the coleps stopped moving, and at the same time the water disappeared from the food vacuole. The coleps became separated from the globulin, and about twelve minutes after the food cup was formed the globulin was excreted.

The results of these experiments leave no doubt of the fine sense of discrimination which ameba is capable of exercising. Not only does ameba discriminate before coming into contact with objects, but also after they are in the food cup and even after they are imbedded in the protoplasm. The experiment recording the ingestion in the same food cup of globulin and a coleps indicates this, for after these substances were imbedded in the protoplasm a coleps was preferred to globulin.

The experiments with egg albumin and globulin, and egg albumin and silicic acid, show clearly that the presence of a substance in solution only is not sufficient to attract ameba, nor to cause ingestion, but that the substance must be actively diffusing from a definitely localized region.[3]

THE EFFECT OF MECHANICAL STIMULATION

It became evident as the feeding experiments went on that movement of food objects is an important factor in ingestion, and sometimes indeed a determinining factor. A number of experiments were then projected to see especially what the effect of water vibrations is upon ameba, and whether vibrations of themselves are capable of causing a definite change in behavior.

It is to be regretted that but few drawings can be presented in illustration of the gradual change in behavior that is produced by mechanical stimulation; but it was impossible to make a series of drawings for each experiment, as was done in the other cases, for the drawing hand of the experimenter was employed in vibrating the needle. Consequently with the exception of one experiment—194-197—which is represented by memory drawings made immediately after the experiment, only the final stages are illustrated by camera lucida figures. The different kinds of objects used in these experiments are fairly representative. Several kinds of insoluble indigestible substances, as well as food substances, were employed.

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[3] There is some evidence here that two particles of different degrees of attractiveness when encountered separately, are reacted to, when lying close together, as one (the more attractive) being attractive and the other (the less attractive) repulsive.

The effect of vibrating food particles.—A small fragment of an ameba was placed in the path of an A. proteus. Pseudopods were sent out toward the fragment, but all of them were soon withdrawn—198-205. The fragment was then allowed to roll down the side of the ameba, whereupon ingestion followed at once—206. It is certain that the mechanical stimulation produced by the rolling fragment hastened ingestion.

An A. dubia was then tested ten times with grains of globulin, but only one was eaten, the seventh. On the eleventh trial a piece of globulin was laid against a newly formed pseudopod and agitated with the point of a glass needle. A food cup was promptly formed and the globulin apparently ingested—207. Five minutes later the ameba moved on, leaving the globulin behind in about the same place—210. It had not been completely surrounded by protoplasm. The formation of the food cup in this case was caused by the vibration of the globulin.

Another A. dubia that reacted rather indifferently toward globulin, although the globulin was finally eaten, and quite indifferently toward ovalbumin, iron and fibrin, was tested with a grain of fibrin agitated with a glass needle. A food cup was formed and the fibrin apparently ingested at once in a food cup containing a large quantity of water—211. The ameba became quiet for a minute and a half and then moved off in the original direction, leaving the fibrin behind, four minutes after the formation of the food cup—212-216. The fibrin was probably not completely surrounded by protoplasm. The formation of the food cup was caused by the vibrations of the fibrin.

The effect of vibrating alga filaments.—One of the most illuminating experiments bearing on the general problems of mechanical stimulation is the following: A raptorial ameba which had reacted indifferently to capillary tubes filled with peptone solution was gently stimulated mechanically by the free ends of three thin oscillatoria threads wrapped around a glass needle. Stimulation at the posterior end produced a prompt reversal of streaming. When stimulated at the newly formed posterior end, streaming was again reversed. In this way the direction of the protoplasmic current was reversed eight times in succession, the current always moving toward the point of stimulation, without bringing the ameba away from its original location. Figure 217 shows the position of the ameba while the protoplasmic current was changed four times. The sides of the ameba were then stimulated at various places with the alga threads and at each point a pseudopod was thrown out. If the stimulating was done properly, food cups were begun at these pseudopods. Partial or complete food cups could be formed at will, depending upon the character and continuance of the stimulus. In short, all the ordinary items of positive reacting, from simple movement toward a stimulus to the prompt and complete formation of a typical food cup, could be produced by varying the intensity, frequency, and character of the stimulus. The mechanical stimuli proceeding from the alga threads were probably the only ones concerned in producing the reactions described, for the bottom of the dish was strewn with broken oscillatoria filaments, over which the ameba frequently flowed without changing its behavior. It was only when the filaments were agitated in contact with the ameba, or nearly in contact with it, that the ameba responded with a positive reaction. The efficiency of this sort of stimulation lies doubtless in the fact that the great flexibility of the alga threads permits one to simulate to a high degree the movements of small living organisms.

An experiment similar to this one gave almost identical results. A large binucleate A. proteus that had reacted indifferently to globulin grains or eaten them imperfectly was stimulated with the alga threads and the response was the formation of a complete food cup—FC_1, 220. The ameba was stimulated again and another food cup was started, FC_2. A grain of globulin was then dropped into the partly formed food cup and upon further stimulation the food cup closed completely. The globulin was retained for over two hours, when observation was terminated. The first food cup which was formed, it is interesting to note, remained almost undiminished in size for over two hours. It remained much longer than if it had contained food.

In another experiment of a similar nature the glass needle was used without any alga threads or anything else on it—194. The point of the needle was agitated near, *but not in contact with*, an A. proteus. A pseudopod was promptly started in the stimulated region—195, and it attained to considerable size and finally formed itself into a food cup, which was, however, not completed—197. The needle at no time touched the ameba. This experiment, in connection with the preceding ones, shows that *a purely mechanical stimulus is sufficient to set in operation the ameba's feeding mechanism.*

The effect of vibrating insoluble indigestible particles: Glass.—A clean piece of glass was laid near an A. dubia and slightly agitated with a clean glass needle—226. The glass particle was promptly ingested in a typical food cup with a large amount of water. The ameba did not undergo a period of rest but kept on moving forward and in six minutes the glass was excreted—232. It had been completely surrounded by protoplasm. Five minutes later the same piece of glass was again agitated with a glass needle—234. Again the glass was ingested in a typical food cup. Three and one-half minutes later the glass was excreted—237. Another trial with the same piece of glass provoked the formation of a food cup until it was about three-fourths completed, then it was retracted—238. Two further trials produced visible responses, but no complete food cup was formed. The ameba became increasingly indifferent toward the artificial stimulation with each succeeding trial.

Silicic acid.—An A. dubia was stimulated with oscillatoria threads until a food cup was partly formed, then a grain of silicic acid was placed in it and stimulation with the alga filaments resumed—240. The food cup closed up apparently completely, for three minutes after the closing of the cup the silicic acid was actively thrust out as a piece of undigested food material might have been thrown out—244.

Carbon.—A fragment of purified carbon was laid on the back of a raptorial ameba—245. The carbon was raised up by the protoplasm immediately underneath it, but very soon thereafter it rolled down the side of the ameba. A large pseudopod was then sent out over the carbon but no distinctive food cup was formed. When the ameba was forcibly rolled over, it was found that the carbon adhered to the ameba. No attempt had been made to surround it after the psuedopod was laid over it.

Indigotin.—A piece of indigotin was laid in front of an A. dubia and agitated with a glass needle—247. The indigotin was eaten by means of a typical food cup containing a large quantity of water. The ameba moved on in the original direction. Nine minutes after the indigotin was ingested, it was left behind. It is uncertain whether the indigotin had been completely ingested.

The experiments recorded in this section demonstrate conclusively that amebas respond positively to mechanical stimulation. Food objects when mechanically agitated, are more readily eaten than when lying quiet, and in many cases food objects are not eaten at all unless they are in motion. Further, insoluble objects, like glass, are not eaten when lying quiet, but when agitated properly they are readily eaten. It is not necessary for a solid object to come into contact with the ameba in order that a food cup may form; vibrations of the water are quite sufficient to produce the feeding reaction. A chemical stimulus is therefore entirely unnecessary in order to set off the feeding reaction. Movement is not only a contributing factor but it is in itself an efficient factor in calling forth the feeding process.

It will be noted that when vibrated particles are eaten, they are seldom retained for more than a few minutes, whether they are of food value or not. The reason for the speedy excretion of such particles is that the chief, if not the only quality of the particle which incited the feeding process, movement, disappears when the food cup closes, for mechanical vibration is then no longer possible. Since the most attractive quality suddenly disappears, the feeding process stops before it is entirely completed. The formation of a food cup resembles to some extent a reflex act: when an agitated particle of glass is eaten, the formation of the food cup continues for some time after the vibrations have ceased. The formation of food cups is due to a racial habit which is guided to a greater or less extent by circumstances attending the formation of a cup at any particular time. Since circumstances vary greatly, one observes great diversity in the behavior toward particles which produce positive reactions.

Whether the swallowed particle is retained or speedily excreted is largely independent of the character of the feeding reaction. The food cup may have been perfectly formed and yet the particle inciting it may be speedily excreted; or on the other hand, the food cup may have been very imperfect, but the particle may be retained. The retention of a vibrated particle in the ameba seems to depend on qualities other than those which caused ingestion. What such qualities are cannot be definitely stated. The composition of the particle seems to have relatively little to do with it, for food particles like globulin are frequently thrown out at once, while glass is always thrown out; and cholesterin, presumably an indigestible substance, was in one case retained for over and hour and a half. The condition of hunger in the ameba is one of the most important factors. But whatever the factors are which control retention, it is certain that they are not the same as those conditioning ingestion.

DISCUSSION OF EXPERIMENTAL RESULTS

Choice of food.—What is choice? This is a very troublesome concept in science. We need some such word as choice in describing the reactions of animals in order to avoid hopelessly confusing circumlocutions, and yet it seems impossible to give a satisfactory definition of choice from an objective point of view. Since I wish to discuss particularly the phenomena of choice of food in this paper, I shall undertake to explain how I use this word.

Choice has been used to label a process by which a certain state of matter in a system is brought about. More restrictively, it has been used to designate exclusively the end result of such a process, the state of matter after the process has ceased. It is obvious, without illustration, that these two meanings of the word are quite distinct from each other and that they can conveniently be qualified by using, respectively, the phrases " process of " and " result of " choice. The word choice is also sometimes used to describe such processes as, for example, the action of a magnet upon a mixture of sand and iron filings. This is an unfortunate use of the word and two objections may be urged against this usage: first, an equally intelligible description of the action of the magnet can be given without the use of the word choice; second, choice might with equal propriety, be applied to every movement of matter in the universe. It is therefore a hindrance to clear thinking to use the word choice as descriptive or nominative of such processes as these.

Again, the concept of choice is frequently restricted to processes observed in organisms, that is, to conscious processes. This view, although of the greatest interest, is very difficult to consider from our present objective experimental point of view, since it would be necessary first to determine whether an animal whose power of choice is in question, possesses consciousness.

The concept of choice is thus seen to occupy a difficult position in science. If a process in organisms can be described as a sequence of events, we may adopt the view that we do not need the word choice in the description of these events; if, on the other hand, a process of choice cannot be described as a sequence, we cannot from the point of view of objective science use a metaphysical concept—consciousness—as a directive force to explain the phenomenon, but must conclude that some of the events in the chain of sequences are still unknown.

Perhaps the chief objection to the use of the concept of choice is that it insistently calls to mind a *relation* existing between, for example, an ameba and some particles which it senses. The *relation* between the ameba and the particles is made to occupy a more important position in the mind than either the ameba or the particles by themselves. The concept is strongly metaphysical, for the instant one seeks for a relation between phenomena one steps into the borderland of metaphysics. A thousand and one other concepts without which we could not possibly get along in science are just as truly metaphysical, but for various reasons we have fallen into the habit of not noticing this characteristic.

Again, the concept of choice originates almost wholly from subjective material, and in ordinary usage it has first of all a subjective meaning. It is supersaturated with anthropomorphism. Let us say that a man chooses an apple from among some oranges. How would these phenomena be related objectively without connoting a subjective process? A kinematographic record even, without any words at all, would be certain to suggest a subjective process. But although we ordinarily thus think of the subjective process, nevertheless if the same events should be made known to us in a paper on animal or human behavior, we would disregard the subjective meaning and center attention only on the objective phenomena. It is, in short, the meaning we are after and the point of view, not the words merely.

To some investigators of behavior such words as selection, choice, etc., are anathema. They would avoid them as they would the plague. But they themselves do not wholly succeed in avoiding them. How would the idea: The ameba selects its food—be rendered on this view? This idea could conceivably be presented, as in the case of the man selecting an apple from among some oranges, by a kinematograph without the use of a word. But would the general impression on the mind be any different, i.e., would it be devoid of subjective elements? It is just as anthropomorphic to say that the ameba eats globulin and leaves carbon, as to say, the ameba expresses choice between globulin and carbon (eating the former and not the latter).

Briefly then, the word choice serves for two purposes. First, it is used as a hypothesis, as a tool of research. It postulates a certain kind of relation which is to give direction to investigation. All except haphazard investigation proceeds in this manner. Second, its use is indispensable for brief and intelligible description; but any subjective connotation which the word may call forth should be disregarded by the reader unless the author specifies definitely otherwise. It is in this latter sense that the word is used *in the descriptions in this paper.*

In a former paper ('10) I demonstrated that the ciliate stentor is capable of exercising very nice discrimination among the various particles which are carried to its mouth by its cilia. Not only is the discrimination between food and indigestible particles (excepting carmine) very precise, but even among food particles themselves, certain organisms being eaten and others rejected. This is particularly noticeable when the stentors are partially satiated.

Now ameba discriminates with equal or perhaps greater precision. Excepting carmine, no indigestible substances are eaten unless agitated. Of the various things eaten, living organisms, such as flagellates, coleps, etc., come first in point of preference. Then comes globulin, grain gluten, carmine, and tyrosin. Less attractive than these are: aleuronat, fibrin, lactalbumin, ovalbumin and keratin, and peptone in solution. Digestible substances that are eaten only occasionally are soluble egg white, solid egg white, uric acid. No starch, lecithin, silicic acid, carbon (excepting in one case), sodium chloride, iron, cholesterin, etc., were eaten unless agitated. Sand grains were never eaten under my observation, and I have never seen " numerous " sand grains inside of amebas from wild or laboratory cultures. It will be recalled that sand grains are frequently referred to in text books and elsewhere as " typical " contents of the ameba's body.

How can these preferences be explained? As far as can be told at present there is no single quality possessed by all the substances which ameba eats, which might be looked upon as the basis of selection; nor do the refused substances possess a common quality which causes amebas to leave these substances alone.

Excepting carmine, all the substances which ameba readily eats are (presumably) digestible, though only two were actually tested in this respect: globulin and grain gluten. But a number of substances which are digestible, such as for example gelatin, egg albumin, fibrin, etc., are eaten only very occasionally or not at all. Of the lifeless solid substances, those which are the more soluble (excepting gelatin and egg albumin, which are very soluble, and globulin which is said to be insoluble) were the more readily eaten. But it is possible that in the case of globulin impurities were present, or that the salts in the water caused slight solubility. The attractiveness of carmine and of lead oxide, and the general indifference toward zein, fibrin, keratin, etc., might be due to the solubility of the former and the insolubility of the latter. Tyrosin is the only rapidly dissolving substance eaten. It is very attractive, but it seems that its rapid rate of solubility is slightly disagreeable or injurious. But there are still several items of behavior that cannot be explained even if an essential part of the basis of selection among lifeless substances should be the rate of solubility. Thus, why should the soluble proteins: egg albumin and gelatin, be passed by with indifference? Or what explanation could be assigned for the fact that solids such as tyrosin and carmine call forth feeding reactions very readily when these substances are in the actual process of dissolving, but if a capillary tube filled with solutions of these substances, is presented, the feeding reaction is not produced? It is clear that neither solubility as such nor the rate of solubility determines in all cases whether a lifeless substance shall be eaten or rejected.

The opinion has become quite general that the chemical constitution of substances determines whether an animal will eat them or not. This view, however, has no experimental support; but on account of its general acceptance, especially as applying to unicellular forms, it may be profitable to examine it in some detail.

Just how can a substance affect a sense organ? Apparently only in two general ways: its molecules or ions may combine chemically, temporarily or permanently, with a part of the sense organ; or, some sort of physical energy radially propagated from the sensed particles may produce physical changes in the sense organ. If a substance affects a sense organ by uniting with it chemically, such sensations as might result therefrom should be related in some way with the chemical constitution of the substance, and the sensations should vary in some way as the composition of the stimulating substance varies. Such a sense organ would mediate true chemical sensations. It would seem that all the elements of at least a few compounds should be represented in consciousness, by a chemical sense organ, when they are tasted or smelled. But this never happens in man. The taste or smell of a substance of a given concentration, on homogeneous sense organs, is always a simple sensation, such as proceeds from a simple stimulus. There is no evidence from the psychological side, as it is recognized that there is none on the physiological, that organs of taste or smell sense the chemical composition of substances. But on the other hand, there is some evidence that physical qualities are sensed by the distinctive organs of taste and smell as is shown by the possibility of stimulating the taste buds by electricity so that there are produced sensations of sweetness, acidity, etc., depending upon the particular buds stimulated. It is possible therefore to stimulate a sense organ of taste by means of chemicals in solution as well as by electricity, a physical stimulus. But the effect of a chemical on a sense organ is not at all the same thing as a chemical effect on a sense organ.

But this distinction is not always clearly drawn.

Metalnikow, in his very interesting and extensive paper on the feeding habits of paramecium, as an important example, does not make very clear the distinction between reactions to physical and to chemical qualities, although he asserts that the chemical nature of a substance determines whether it will be eaten by paramecium. Let us therefore examine the experimental results and arguments of Metalnikow, in the light of what was said in the preceding paragraphs, to see whether he is justified in stating that paramecium selects its food upon a chemical basis.

Paramecia eat powdered glass, sulphur, chalk, aluminum, sepia, as well as egg yolk, milk, olive oil, and other digestible substances (see p. 398, table 1.), but he says:

> Toutes ces expériences nous montrent avec certitude que l'absorption par les Infusoires des corpuscles suspendus dans l'eau et la formation des vacuoles digestives dépend de la nature chimique de la substance dont sont formés ces corpuscles. Sans aucun doute les Infusoires sont capables de distinguer les différentes sortes de nourriture qui peuvent se trouver à leur portée.
>
> Il est intéressant de vérifier à present si les infusoires peuvent absorber les différentes substances toxiques insolubles dans l'eau. A cet effet, les Infusoires ont été nourris de différents sels insolubles de mercure et d'arsenic, et j'ai été étonné de voir que ces sels sont assez vite absorbes par les infusoires qui arrivent même à former quelques vacuoles digestives; ces infusoires perissent ensuite bientôt. Mais il ne faut pas oublier qui même l'homme et les animaux supérieurs ne sont pas toujours capables de distinguer les substances toxiques, si ces substances sont dépourvues de mauvais goût (pp. 401–402).

It is evident that Metalnikow speaks here of selection by the feeding mechanism, and not of histonic selection, that is by the digestive mechanism of the tissues.

It is difficult to see how paramecia can be said to distinguish between substances on a chemical basis when indigestible and insoluble substances as well as digestible and soluble, are eaten to about the same extent.

Choice based upon chemical qualities is qualitative; each chemical substance must be conceived of as acting specifically. According to this conception, when the sense organ is stimulated the quality of the sensation is exactly expressible; it cannot vary excepting as to its amplitude or continuance. There can be no doubt as to the exact nature of the stimulating object. We would therefore expect an animal capable of choosing on this basis, to choose with great precision. We would certainly expect much more precise selection even if the power of selection was very crude, than is shown in Metalnikow's first table. For according to this table glass and sulfur are eaten apparently as readily as milk or starch and eighty per cent as freely as olive oil (table 1, culture C).

Organismal selection in paramecium seems therefore to be extremely crude; in fact it can hardly be said to exist at all under ordinary conditions.

But even if paramecium discriminated between digestible and indigestible substances, the supposition that it did so on a chemical basis is open to question. For it is assuming a great deal when it is said that paramecium becomes aware in some way of the diverse chemical structure of starch, milk, various bacteria and bacilli, leukocytes, yeast cells, egg yolk, olive oil, albumins, etc., while these substances are passed back to the mouth by the cilia of the gullet. Now in order that paramecium may become aware of the chemical nature of these several substances, new compounds must be formed in the sense organs of the paramecium (the cilia?) involving a permanent or temporary union of a part or the whole of the molecule of starch, albumin, oil, etc., with some structure in the sense organ, to form, in each case, a definite and characteristic compound which would then serve in some way to set into operation the ingesting mechanism. What the chemical equipment of a sense organ would have to be in order that compounds might be thus formed with all the different substances which paramecium eats, it is difficult to conceive. Metalnikow does not attempt to give an explanation of how selection on a chemical basis might operate; nor to my knowledge do any of the other writers on protozoa, although several refer more or less casually to the selection of food as based on its chemical nature. That it is unnecessary to explain choice of food upon a chemical basis in paramecium or in any of the other protozoa whose feeding habits have thus far been investigated, will be shown by examining the process of selection in ameba.

Recently Lund ('14) published an important paper on the feeding reactions of the large ciliate, bursaria. In this paper Lund discusses the selection of food in bursaria, especially as to whether it rests on a chemical or on a physical basis, and in this connection refers to a previous paper of mine treating of similar questions about the feeding behavior of stentor. It seems however, that Lund did not quite understand my conception of the difference between selection of food on a chemical basis and on a physical basis, doubtless because I did not go into the details of the difference as I conceive it. I have examined his paper carefully but, although he insists that bursaria selects its food on a chemical basis, I have nowhere found a discussion in his paper which sets forth just what he conceives to be a chemical basis as distinguished from a physical, in so far as the selection of food is concerned. I have, therefore, found it of interest to examine his paper in some detail, for it is absolutely essential that the difference between selection on a chemical and on a physical basis be clearly drawn, before we can say that an animal selects its food on either basis.

Lund fed bursaria with yolk of hen's eggs untreated, and stained with various chemicals, employing essentially the methods I used in my work on stentor ('10), and Metalnikow ('12), on paramecium.

Yolk treated with various dyes is eaten less readily than untreated yolk. If NaOH, HCl, saffranin, etc., are added to the culture solutions in varying quantities, the yolk is eaten in decreasing quantity in proportion as the toxic substance is increased in concentration. Temperature also has a similar effect; with a rise of temperature from 0° to 35° C., there is a corresponding increase in the amount of yolk eaten. Beyond 35° C. the temperature becomes injurious. In addition to these experiments, Lund mentions some observations to the effect that carmine, india ink, aluminium, carbon black, cinnibar, etc., are eaten by bursaria (p. 43).

It appears then that bursaria stands between stentor and paramecium (and close to paramecium) as far as concerns its capacity to discriminate in feeding.

From the results of his experiments, Lund expresses agreement with Metalnikow ('12) in so far as the basis of selection is concerned.

But it was shown in the preceding pages that Metalnikow's conclusion that food is selected on a chemical basis is not in agreement with all the facts; and the same criticism to which Metalnikow's conclusions are open, also apply to Lund's. It will therefore not be necessary to go over this ground again. It should be noted however, in this connection that Lund dismisses with a single paragraph, as if they did not bear at all on the question of selection, all the observations he made on the eating of chemically inert substances, such as aluminium, carbon, etc. But it is precisely these observations which most strikingly contradict his notion that selection is made on the basis of the chemical composition of the substances. *How can* *one explain the selection of insoluble substances such as carbon or aluminium, which are eaten, on a chemical basis?*

The experimental results which form the basis of Lund's conclusion admit of another interpretation. The fact that more and more yolk was eaten as less and less of NaOH, HCl, saffranin, etc., was present, does not of course indicate active selection; the presence of toxic substances affected the general bodily condition so that feeding was to some extent suspended. It cannot be inferred that the bursarias " tasted " with the food selective mechanism the toxic substance, and on this account refused to eat less as this substance was more and more concentrated. The experiments with temperature show a feeding gradient that corresponds almost exactly with that obtained in those experiments where toxic substances were employed in varying concentrations. Clearly therefore, there must be other evidence to show that selection is based on chemical constitution; for the observation that chemicals in varying concentrations prevent feeding to a greater or less extent, does not mean that these chemicals were 'tasted' by the mechanism of food selection any more than that the various temperatures, or the electric current, or the mechanical stirring, were tasted. In other words, the feeding mechanism in bursaria, as in many other animals, is affected by stimuli affecting the general bodily condition, as seems to be the case when stimulated by agitating mechanically the medium in which the bursarias live, or by passing electric currents through the medium, etc. In these cases the inhibiting impulses arise in other parts of the body, and are transmitted to the feeding mechanism.

Chemical solutions, when mixed with the medium, also affect the sense organs of the ectoplasm generally, so that feeding may be inhibited without involving the action of the food selective mechanism at all (see Lund, pp. 41, 42). Whether Lund succeeded in localizing the effect of stains absorbed by the yolk grains so that only the food selective mechanism was affected and then not injuriously, is very doubtful; that he did succeed may not be concluded from his experimental results. It is probably superfluous to add that unless one is sure that the food selective mechanism is at any time regulating the feeding mechanism, discussion of the bases of food selection is beside the point.

The distinction between the feeding and the selective mechanisms is not merely academic. The distinction can readily be made in the higher animals, and there are some observations in my paper, viz., those where tyrosin was fed, which show that the distinction is experimentally verifiable in ameba. But the clearest illustration of this point among the lower forms is to be found in stentor.

It follows, then, that those experiments where various temperatures, electric currents, toxic substances, were employed, important as they are of course from other points of view, cannot be admitted as evidence in support of the chemical theory of food selection. And as to those experiments where the yolk was stained and the superfluous dye washed out, it is really doubtful if there is evidence here that bears on the problem of choice of food. The adsorbed dye gradually washed out, according to Lund, in the course of the experiments, and it is, therefore, next to impossible to be sure that only the food selective mechanism is stimulated when a response is obtained; but this, as has been said, is the first essential in investigations on choice of food.

The food selective mechanism is the most delicate mechanism affected by food substances, and it is the last mechanism that tests the particle before it is eaten or rejected. A particle of any substance must not cause a general negative reaction before it affects the food selective mechanism, otherwise the animal cannot express choice as to its food qualities. If the body reacts negatively to a particle (solid or in solution) before the food selective mechanism is affected, the result is choice only between indifferent and injurious substances. That is to say, an injurious substance produces a negative reaction, while all other substances are indifferent. The presence or absence of food qualities is not the basis upon which choice is made under such conditions. As a concrete case we may refer to Stentor caeruleus. So far as we know, the cilia of the disk of stentor are not a part of the food selective mechanism. But they are a part of the feeding mechanism. Food materials, carmine, starch grains, glass, sulphur, etc., brought to the disk by the vortex produced by the membranellae, are all transferred to the pouch and funnel leading to the mouth. But when an injurious substance comes into contact with the disk, a negative reaction sets in. The discal cilia accept indifferent or non-injurious particles and reject injurious substances. But when the particles reach the pouch and funnel, selection is made on a different basis, for here starch, glass and sulphur are rejected, while food particles are eaten. When injurious substances affect the disk feeding is for a longer or a shorter time more or less completely inhibited. The decrease in the amount of food eaten in such a case is not due to activity of the food selective mechanism, for the stimulus resulting in partial or complete cessation of feeding arose in another part of the organism where selection between food and other materials has been shown not to occur. It seems then that choice of food such as is observed for example in stentor and in ameba results from the presence in particles of qualities which *induce* feeding, and not from the presence in other than food particles of qualities which *prevent* the ingestion of these particles.

In so far as selection is concerned, all of Lund's experiments, including those where carmine, cinnibar, carbon and other indigestible substances were eaten, can be explained by assuming that choice is based upon the physical properties of the substances, and that all solid non-injurious particles of handleable size are eaten. But if toxic substances are present, or if the temperature is too low, or if an electric current is present, or if the bursarias are violently agitated, the bursarias are disturbed or injured and not only choice but feeding is suspended to a degree corresponding to the strength of the stimulating agent. This simple explanation covers all the recorded facts of feeding in bursaria, and conforms with the explanation of the selective processes in stentor and paramecium, and to a considerable extent with that of ameba.

It has already been pointed out in several places that A. dubia is readily stimulated by moving objects; and that almost any object in vibratory motion is eaten, whether the particle is composed of glass or carbon, or whether it is a living or a dead organism. So ready is the response of these amebas to objects in motion, that their seldom reaction to motionless objects, or to lifeless objects, is readily overlooked. Thus Gibbs and Dellinger ('08) whose plates II and III indicate that they probably worked with this species, concluded that "Amoeba eats nothing dead."

"The Amoeba shows distinct food preferences; with diatoms and unicellular algae, it takes algae, but when feeding on algae it will leave them to "pursue" ciliates. In the presence of large paramecia, some amoebas leave algae and ciliates to catch these larger forms. Amoeba eats nothing dead. This was observed in the case of dead diatoms and algae cells, of paramecia dead from natural causes, and of paramecia which had been artificially killed. Amoebas do not apparently eat their own species, but were seen to eat amoebas of other species" (p. 240).

As we have seen, however, A. dubia eats lifeless things, though only very rarely (see under carmine, Schaeffer, '16a, '16b under "raptorial" amebas). My observations confirm theirs on reactions toward dead organisms or parts of organisms: none are eaten. Now when it is remembered that in the normal life of an ameba neither carmine nor isolated proteins occur, it is clear that movement in an object is practically the only quality which induces feeding in A. dubia. In other words we have conclusive proof that the chemical nature of the moving eaten object is of no importance whatever in so far as feeding is concerned, and that the quality that actually determines ingestion is clearly a physical quality. The ability to discriminate among substances on a chemical basis while feeding, might, therefore, be entirely absent in A. dubia without affecting its ability to live successfully.

So far as normal feeding is concerned, A. proteus has practically the same habits as A. dubia, in that by far the larger quantity of food consists of living moving organisms, which are selected because of their movement. But it differs from A. dubia in that dead organisms and fragments of isolated proteins, etc., are readily eaten. Here, manifestly, selection is made upon a broader basis. But if all the experiments where motionless objects are eaten are taken together it does not seem possible as we have already seen that choice based upon a single factor could lead to such diversified behavior. Thus if the chemical nature of substances stimulated ingestion (1) carmine would probably not be eaten; (2) solid and soluble egg albumin and gelatin would probably be eaten with avidity; (3) globulin, lactalbumin, ovalbumin, which are said to be insoluble, would be eaten; (4) uric acid would not be eaten; (5) capillary tubes filled with carmine solution and with tyrosin solution would be as attractive as solid carmine and tyrosin respectively; (6) food cups would be formed when the chemical substance was first sensed, instead of after the source of diffusion was reached. Then there is the further general observation that the ameba moves directly toward a stimulating object, if positively attracted. That is, the ameba moves parallel with lines of diffusion radiating from the soluble object; or, if the object is not soluble, along lines of force of another nature propagated in a similar manner. It is clear therefore that for lifeless objects, choice cannot be based on a single factor, nor can it be based exclusively on the chemical composition of the sensed objects.

The ameba seems to be stimulated at several points by a sensed object, and locomotion then proceeds along the line of intensest stimulation. This is a method of reaction directly comparable to that of the higher animals, when stimulated positively by heat from a definite source. The whole ectoplasm (particularly the anterior portion) may be considered as a sense organ capable of receiving stimuli at many points with local reference. That the stimulus itself (for example, a change of surface tension) directly conditions the path of movement seems impossible; for the nature of the responses to stimuli is not at all machine-like, as the experiments abundantly show, and as they would necessarily be if the stimulus directly determined the reaction.

One of the chief difficulties in the way of accepting the hypothesis that food is selected on a chemical basis is the discovery that organismal and histonic selection are not synonymous. This is very significant. Carmine, which is invariably readily eaten, is nevertheless always speedily egested. It seems to make little difference whether the ameba is hungry or nearly satiated, speedy egestion follows the ready eating of carmine. Similar, though not as striking results, are obtained in the behavior of A. dubia toward lactalbumin, uric acid, etc.

Now, if the chemical nature of an object is thoroughly tested at any time by an animal, it is just after it is eaten. The digestive juices then begin to act upon it chemically, and its constitution then determines what will happen to it. In a general way, if the substance is digestible and harmless, it remains in the body; but if indigestible or irritating, it is soon excreted. Now the fact that organismal selection, in many cases, leads to results directly opposed to those of histonic selection, demonstrates conclusively that these two methods of selection do not rest upon the same basis.

Although Metalnikow did not seem to recognize the difference between organismal selection (exercised while feeding) and histonic selection (exercised when the process of digestion begins), his data clearly indicate that carmine, aluminium, powdered glass, sulphur, etc., are as readily eaten as, but more speedily ejected than food particles. The fixed habit of cyclosis in paramecium, and that of egestion at a definite point, serve to obscure this difference somewhat, for it tends to equalize the time during which digestible and indigestible substances are retained in the body. But the fact nevertheless stands out when Metalnikow's tables are closely examined. Thus if tables I and IV are compared, it is observed (table I, culture C) that glass and sulphur are eaten more readily than milk, as readily as starch, and nearly as readily as olive oil; while table IV shows that (in other cultures, it is true) these substances are excreted much sooner than starch, olive oil, or milk. It is quite evident, then, that the ectoplasmic evaluation of substances differs from the endoplasmic, in paramecium as distinctly as in ameba, though not as strikingly, and that choice of food is not made upon the same basis by the ectoplasm and the endoplasm.

Seeing then that organismal selection of food as observed in ameba is not explicable on a chemical basis, one naturally looks to physical properties for the explanation. Is selection based upon physical properties? Unfortunately a complete answer is not yet possible, nevertheless we may consider briefly the direction an explanation of selection on a physical basis would take.

It is not necessary to suppose, in the first place, that each substance to which ameba reacts, stimulates the ameba in a specific way. It is possible that many of the substances as sensed differ from each other only quantitatively in certain physical characteristics. This is, for example, the case in man with most tasting substances. The various sugars and saccharin differ from each other only quantitatively in taste, supposing that the taste buds for sweetness only are stimulated. The same is true for various acids. And as a further illustration one may refer to color vision. Here a large number of quantitatively varying ether vibrations produce specific sensations which are then qualitatively interpreted. Attention may also be called to the fact that man does not acquire a knowledge of the chemical composition of any single substance directly by a sense organ. The nearest approach to obtaining such knowledge is in the smell sensations of the elements chlorine, bromine and iodine; but even with these substances it has been pointed out that the mucous membrane, aside from the olfactory nerve endings, may be stimulated, and that nascent hydrogen may combine with these elements before the sense organ is stimulated. We cannot conclude, therefore, that iodine, bromine and chlorine are sensed in the elemental condition. Now since we do not find any conclusive evidence in man (or elsewhere) that the chemical composition of substances is sensed, not even in a single case, one must, to say the least, feel suspicious of the correctness of the chemical hypothesis. Differences in surface tension, adsorption, rate and direction of diffusion of dissolved molecules, ionization, reflection of light from suspended particles, etc., are probably among the properties which play a part in determining the feeding behavior of ameba. The disturbance due to moving animals in water, which is transmitted as waves of changes of pressure to the ameba, and which, as we have seen, is the most potent stimulus for setting off the feeding reaction, is purely a physical property, and it is not unlikely that the effect of the pressure waves is a change in the distribution of surface energy on the part of the ameba affected. While we are far from explaining all the acts of selection in ameba on a physical basis, a respectable beginning has nevertheless been made, as we have seen in the section devoted to the effect of mechanical agitation.

What has been said about the basis of selection in this section has had reference only to individual acts of selection; the eating of a grain of carmine or of globulin, or the avoidance of a grain of carbon, each taken by itself. A very important element affecting selection in a broader sense, that is, selection as the sum of the feeding behavior of an ameba, has not yet been mentioned. This element is the effect of previous experience.

The importance of this factor in selection is equalled by the variety of ways in which it may express itself. The previous stimulus and response characteristically affects the succeeding response. In some cases the effect is slight compared with the stimulus; in others the effect of the previous stimulus and response is much more important than the succeeding stimulus. Thus in experiments 6–13 (Schaeffer, 1916c) the sensing of tyrosin grains affected the ameba in such a way that the succeeding grain of globulin was treated at first like a grain of tyrosin. But after the ingestion of the globulin, the succeeding grain of tyrosin was treated like the grain of globulin, and promptly eaten. The behavior of the ameba was ordered with definite reference to its past. It is clear that each of these items of behavior, taken by itself, could not be explained. The process of selection cannot be understood by treating in a quantitative manner a number of separate acts of choice. On the contrary, selection must be looked upon as a *connected, developing process involving at least the entire past of the individual ameba.*

SELECTION OF FOOD IN STENTOR AND PARAMECIUM AS COMPARED WITH THAT IN AMEBA

In this section are summarized the chief facts bearing especially on the selection of food in stentor, paramecium and ameba. A comparison of the main results of investigations on these organisms serves to give a better conception of this problem of choice of food, I believe, than can be had in any other way. Incidentally, such a comparative study gives also a hint as to the probable path of development in a species of whatever method of selection may be present in that species. The reason for selecting these three organisms is that they serve as types of three methods of selection, and what is equally important, the food selective processes are better known in these three organisms than in any other lower forms.

Paramecium. Paramecium feeds on bacteria and other very small particles, but bacteria form much the larger part of the normal diet.

A very great number of particles, hundreds of thousands or millions, must be eaten every day in order to maintain life.

If the particles were tested individually, an enormous amount of time would be consumed in the process, and there would not be sufficient time to eat the optimal amount of food. The ingestion of particles of sand, debris, mud, silt, etc., if each particle were tested individually, could therefore not be considered an advantageous reaction, since it would entail a dangerous decrease in the amount of food eaten. In times of very slightly muddy water, paramecia would starve to death if careful selection should be practiced, for the time consumed in rejecting silt would permit but very little food to be eaten. It is therefore of advantage to paramecium not to examine finely divided particles individually, since the maximum amount of food can be obtained under normal conditions without selection, and the few particles not of food value that may be ingested are harmless.

It may be supposed then that paramecium has lost the power to a greater or less degree, of selecting its food as it is brought to its mouth. Everything that is finely divided is eaten, whether poisonous or not. Metalnikow's experiments ('12) where powdered glass, sulphur, aluminium, arsenic salts, etc., were eaten, prove this point very strikingly. The physical quality of solidity of a substance is sufficient to set off the ingesting mechanism, provided the particle is of such size that paramecium can take it down the gullet.

The positive responses of paramecium to many chemicals, as worked out by Jennings and others, may be interpreted as a reaction to a stimulus which has become associated with the presence of food, most of these chemicals probably stimulating paramecium in a manner similar to carbon dioxide, which is always found where bacteria are found, and with which paramecium continually comes into contact. It is not necessary to suppose that each of the positively stimulating chemicals has a characteristic stimulus. The reactions do not indicate this, and it is quite an adequate explanation to assume that the sensation is the same in quality for most or all of the chemicals in solution producing positive behavior. The intensity of the sensation may vary, however, for different substances, as it seems to vary with the degree of concentration of any one of certain chemicals. The fact that paramecium reacts to chemicals does not at all indicate that the composition of the chemical substance is sensed by the paramecium, or even that a qualitatively characteristic response is produced in the sense organs by each substance. It is likely that some physical property, common to carbon dioxide and to other substances causing positive behavior, stimulates the paramecium. There are a number of instances in which it has been definitely shown that a physical quality of an object stimulates amebas, stentors and paramecia, but there is no case where it has been definitely shown that a characteristic response is due to some chemical effect. The reactions of paramecium, therefore, can be consistently and adequately explained by assuming that physical qualities act as the stimuli.

It remains to mention that selection of food is accomplished roughly by the avoiding reaction. If a paramecium comes to a locality where an injurious chemical is dissolved in the water, the paramecium avoids the locality and all solid particles in it. If, however, an attractive chemical such as carbon dioxide is present, the paramecium enters the water where the diffused chemical is and eats all the particles of proper size there without expressing any choice among them, for carbon dioxide is not injurious in dilute solutions. Inside of the funnel or gullet of paramecium there is practically no selection, though Metalnikow has shown that the power to discriminate may be developed very appreciably by proper experimentation (Metalnikow, '12).

Stentor caeruleus. The blue stentor feeds on small particles such as bacteria, and also on larger forms such as ciliates, flagellates, rotifers, zoospores, unicellular algae, etc. It is difficult to say what the normal diet of stentor is, but it may be mentioned that laboratory cultures can be raised very successfully on bacteria and flagellates such as chilomonas. The number of particles eaten per day depends of course upon the size of the particles. Ten paramecia may be quite sufficient, but it would require thousands of flagellates and millions of bacteria, if either of these kinds of organisms were eaten exclusively.

Stentor has a food sorting mechanism by means of which any particle can be ingested or rejected ' at will.' The selective mechanism acts with great precision, especially when the particles are of appreciable size. In such case relatively few particles need to be eaten to maintain life, and there is consequently sufficient time for careful selection of individual particles.

It is reasonable to suppose that it is advantageous to stentor to sort out the food particles from all that are brought to it, whenever these particles are of large size.

Stentor still possesses the power to choose its food especially where larger particles are concerned. But indigestible material may be eaten when very hungry. Very small grains of indigestible material (carmine) are refused to a much greater extent when food is present than when absent. Large particles of glass, sulphur, starch, are consistently refused.

The experimental evidence makes it highly probable that selection is based upon the physical (tactual) properties of the substances (Schaeffer, '10).

As compared with paramecium it is true that stentor is capable of much nicer discrimination in the laboratory tests, but it is probable that in natural surroundings the methods of paramecium in food selection are quite as well fitted as stentor's for successful living, if not more so.

Amoeba proteus, *A. dubia*, *A. discoides*. Ameba feeds on large solid particles, living or dead; protozoa, protophyta, rotifers, zoospores, masses of zooglea, dead masses of protoplasm, etc. Whether ameba takes in liquid food is not known.

Usually only one or two particles are eaten at a time. Several particles of such forms as urocentrum, paramecium, desmids, may be sufficient for a day's feeding; or if the organisms are small, such as chilomonas, several hundred are eaten. There is therefore sufficient time for selection in every case.

Ameba eats normally only digestible matter. The degree of precision of selection in ameba compares favorably with that in stentor.

Ameba still possesses the power of selecting its food.

Selection is based, in many cases, upon the physical properties of objects such as, for example, movement.

Ameba rejects an undesirable object by moving away after coming into contact with it; or by not moving toward it if the stimulus, such as very violent movement, is too intense.

Comparing the processes of choice in food in these three protozoans, we observe that in paramecium an enormous number of particles must be eaten daily to sustain life, so many particles in fact that a process of selection could not be applied to each individual particle. And experiment shows that selection of food is almost completely suspended in this organism. Stentor feeds on large particles as well as on small ones, such as bacteria. Stentor can live readily on a few large particles eaten daily, and there is abundant time for careful discrimination. Experiment shows that stentor is capable of very nice discrimination. Ameba eats only large particles and in this organism also very nice discrimination is exercised. In all these protozoans selection is based upon physical characters of the food objects rather than upon their chemical constitution. Thus, among amebas, movement of an object is in a very large number of cases an adequate stimulus; stentors seem to react to a composite stimulus formed of several qualities such as weight, surface texture, shape, size, solubility, etc.; while paramecia seem to be sufficiently stimulated by the solidity of particles of small size.

Not only has the extension of the sensing range of food objects been based on the physical characters in these protozoa, but also in most if not all of the higher animals as well. Thus all seeing animals depend more or less on the physical characters of objects as a basis for choosing their food. After objects are selected by sight as suitable for food, another test is made of them by the sense of taste, or touch, or smell, or all of them together. But there is at least one group of animals that depend on sight almost, if not quite exclusively—the anura. Only moving objects are snapped up, and these are usually snapped up with such vigor that even if they are found disagreeable in the mouth, such as hairy caterpillars are, for example, they often cannot be ejected. A frog would starve in the presence of motionless food objects. It is likely also that in many seed eating birds, taste and smell play a very minor part in food discrimination. There has, in short, been a tendency in animals generally to increase their sensing range of food by reacting to distinctive physical qualities, especially such as can be sensed at a distance, until in some forms, according to experimental evidence, none but physical qualities are concerned in selection.

SUMMARY

1. Ameba is capable of exercising very nice discrimination in feeding between two particles of different composition—one digestible, the other not—lying very close together. When the particles stick together slightly, the food cup in some way separates them so that the food particle comes to lie inside the food cup while the other particle is actively pushed to the outside. The ameba not only expresses choice between particles of different composition under special conditions therefore, but if the conditions are such that a choice cannot at once be made, the ameba can change the conditions (separate the particles) so that a choice may then be made.

2. The experiments with two particles of diverse composition

indicate, in conformity with the results recorded in my previous papers, that some physical disturbance propagated radially from the source of stimulation is an essential factor in determining the direction of movement of the ameba.

3. No definite statement can be made regarding the basis upon which choice in general is made. In a general way only digestible substances are eaten, but some digestible substances are refused (zein, gelatin) and some indigestible substances (carmine, india ink) are readily eaten. It can be stated however, that the basis of selection is not chemical in any known case and that in several important cases selection is based upon physical properties.

4. Movement of a particle is one of the most important, if not the most important food quality a particle can possess. Particles of glass, which are never eaten when lying still, are readily eaten when agitated.

5. The experiments with mechanically agitated particles bring out very strikingly the difference between organismal and histonic selection. The ingesting and the digesting mechanisms differ profoundly as to the food value of a particle of agitated glass, for example.

6. Observation and experiment indicate that amebas might possibly be able to exist and propagate indefinitely in nature if they selected their food on the basis of movement alone.

7. The experiments show that, in many cases, past experience in receiving stimuli or in feeding is of more importance in selection than the nature of the stimuli received from a present object.

Many individual acts of selection cannot therefore be explained when standing alone, but only when the ameba's past, especially its immediate past, is known. Selection is therefore a historical process. The main factors, then, that enter into selection are physical and experiential.

BIBLIOGRAPHY

GIBBS, D. AND DELLINGER, A. P. The daily life of Amoeba proteus. *Amer.* 1908. *Jour. Psychol.*, vol. 19, pp. 230–241, 7 figs., 3 plates.

LUND, E. J. The relations of bursaria to food. *Jour. Exp. Zool.*, vol. 16, pp. 1914. 1–52, 8 figs.

METALNIKOW, S. Contributions a l'etude de la digestion intracellulaire chez les 1912. protozoaires. *Arch. de Zool. Exp. et Gen.*, (5e Serie, T. IX) vol. XLIX, pp. 373–498, 3 figs., 2 plates.

PENARD, E. Faune Rhizopodique du Bassin du Leman. Gènéve, pp. 714.
1902. Numerous figures.
RHUMBLER, L. Physikalische Analyse von Lebenserscheinungen der Zelle. *Arch.*
1898. *f. Entw.-Mech.*, Bd. 7, pp. 103–350, 100 figs., 2 plates.
1910. Die verschiedenartigen Nahrungsaufnahmen bei Amöben als folge verschiedener Colloidalzustande ihrer Oberflächen. *Arch. f. Entw.-Mech.*, Bd. 30, erster Teil, pp. 194–233, 9 figs.
SCHAEFFER, A. A. Selection of food in Stentor caeruleus Ehr. *Jour. Exp. Zool.*,
1910. vol. 8, pp. 75–132, 2 figs.
1912. Selection of food among lower animals. *Trans. Tenn. Acad. Science*, vol. 1, pp. 35–43, 2 figs.
1912. Contributions on the Feeding habits of Amoeba. *Trans. Tenn. Acad. Science*, vol. 1, pp. 59–64, 3 figs.
1914. Feeding habits of Amoeba. *Science*, vol. 39, p. 472.
1914. Reactions of Amoeba to light. *Science*, vol. 39, p. 474.
1916a. On the feeding habits of ameba. *Jour. Exp. Zool.*, vol. 20, pp. 529–584, 6 plates.
1916b. Reactions of ameba to isolated and compound proteins. *Jour. Exp. Zool.* Vol. 22.
1916c. On the reactions of ameba to carbon and glass and other insoluble substances, and to some very soluble substances. *Biol. Bull.* vol. 31.
1916d. Concerning the species Amoeba proteus. *Science*, vol. 44, pp. 468–469.
1916e. Notes on the specific and other characters of Amoeba proteus Pallas, Leidy, A. discoides nov. spec., and A. dubia nov. spec. In Press. *Protistenkunde.*

EXPLANATION OF PLATES

The figures are camera lucida drawings of sample experiments taken from the laboratory notes without alterations. The camera lucida was attached to the long arm of a Zeiss binocular microscope. Eyepiece 4 and objective a_3 were used, giving a magnification of 65 diameters. A scale by means of which the size of amebas and of test objects can be estimated is shown on plate 4.

The figures are numbered serially from 1 on for reference. These numbers are placed inside the figures. They are to be looked upon as labels only. They have no other significance. An x following a number, as 13x, indicates the end of the experiment illustrated by figures 1 to 13 inclusive. A new experiment starts with figure 14 and ends with figure 25x, and so on. A number followed by xx indicates that the next experiment was performed upon a different ameba. Thus figures 1 to 66xx represents the results of a number of experiments upon the same ameba. With figure 67 a new ameba was employed, and so on. The order in which the figures were drawn is represented by the serial numbers for all the figures in any one experiment, and in nearly every case for all the experiments performed on any one ameba.

The time of the beginning and the end of each experiment is given in hours and minutes. In some cases the time of drawing of each figure is also given, and where it is not given it may easily be computed.

The arrows show the direction of active protoplasmic streaming. The arrows in the last figure of each experiment denote the direction the ameba took in moving away from the test object.

The test objects are labeled in abbreviated form. See table of abbreviations below. For quick and correct reference the test objects are connected with the proper amebas by leader lines. These lines have no other significance.

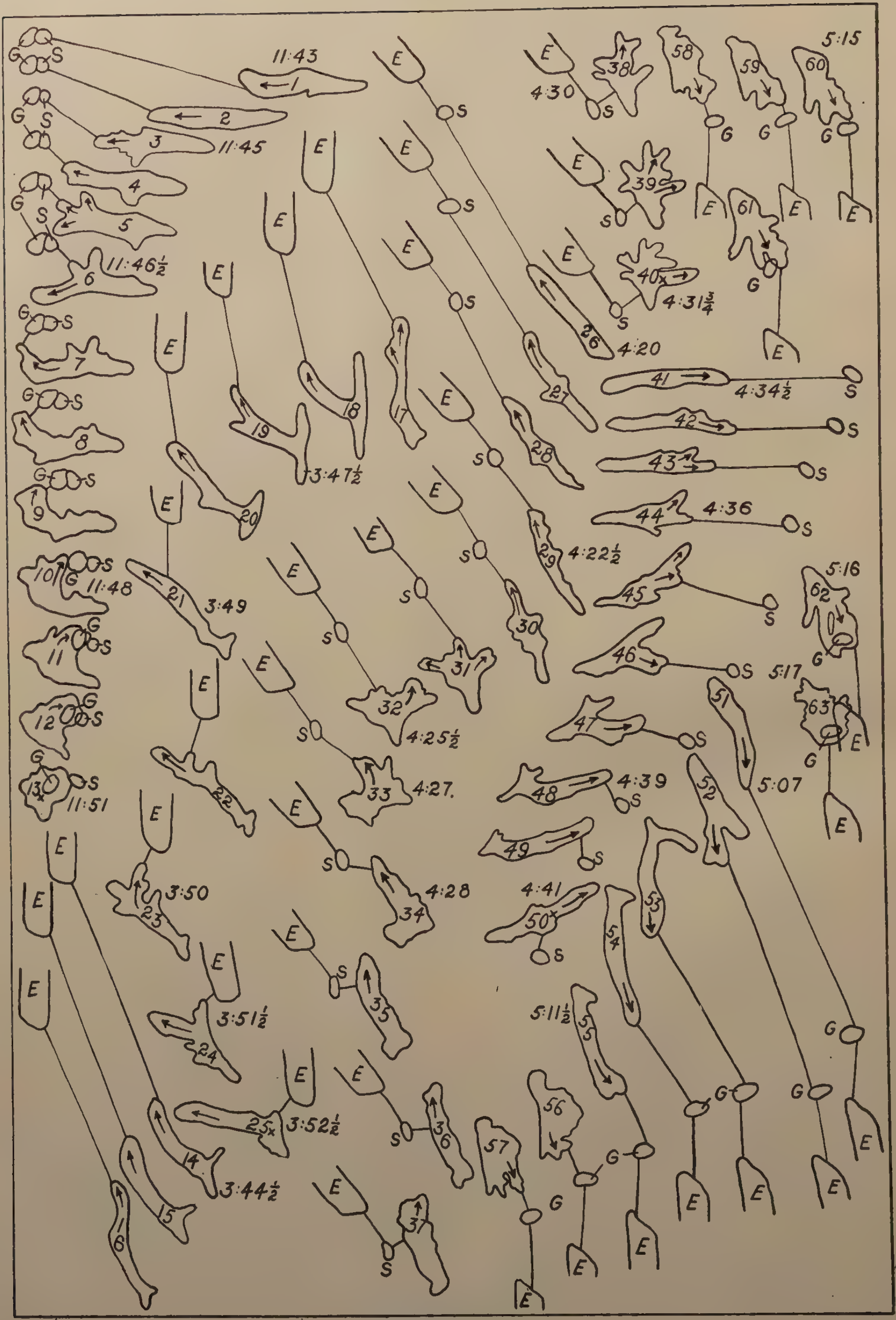
All the work was done facing a north window. All the figures were drawn in the same position in the laboratory and on the plates. The top of each plate therefore points toward the north. This is worth noting from the point of view of the possible influence of light on the behavior of ameba.

It will be noted that there are slight differences in the size and shape of the same test object as drawn in the figures of any single experiment, even if the object was not rolled around by the ameba. The explanation for these differences lies in the speed with which the drawings had to be made in order to catch important items of behavior. As a rule the parts of the ameba lying nearest the test object received the most careful attention and were drawn first; the posterior parts of the ameba and the test object were drawn last.

For detailed explanation of figures see pages 221 to 231 of the text.

TABLE OF ABBREVIATIONS

AM,	ameba	GG,	grain gluten
CA,	carbon	GL,	glass
COL,	coleps	H,	hematin
E,	egg albumin	IN,	indigotin
F,	fibrin	LE,	lecithin
FC,	food cup	S,	silicic acid
G,	globulin	U,	uric acid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4:22½
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4:28
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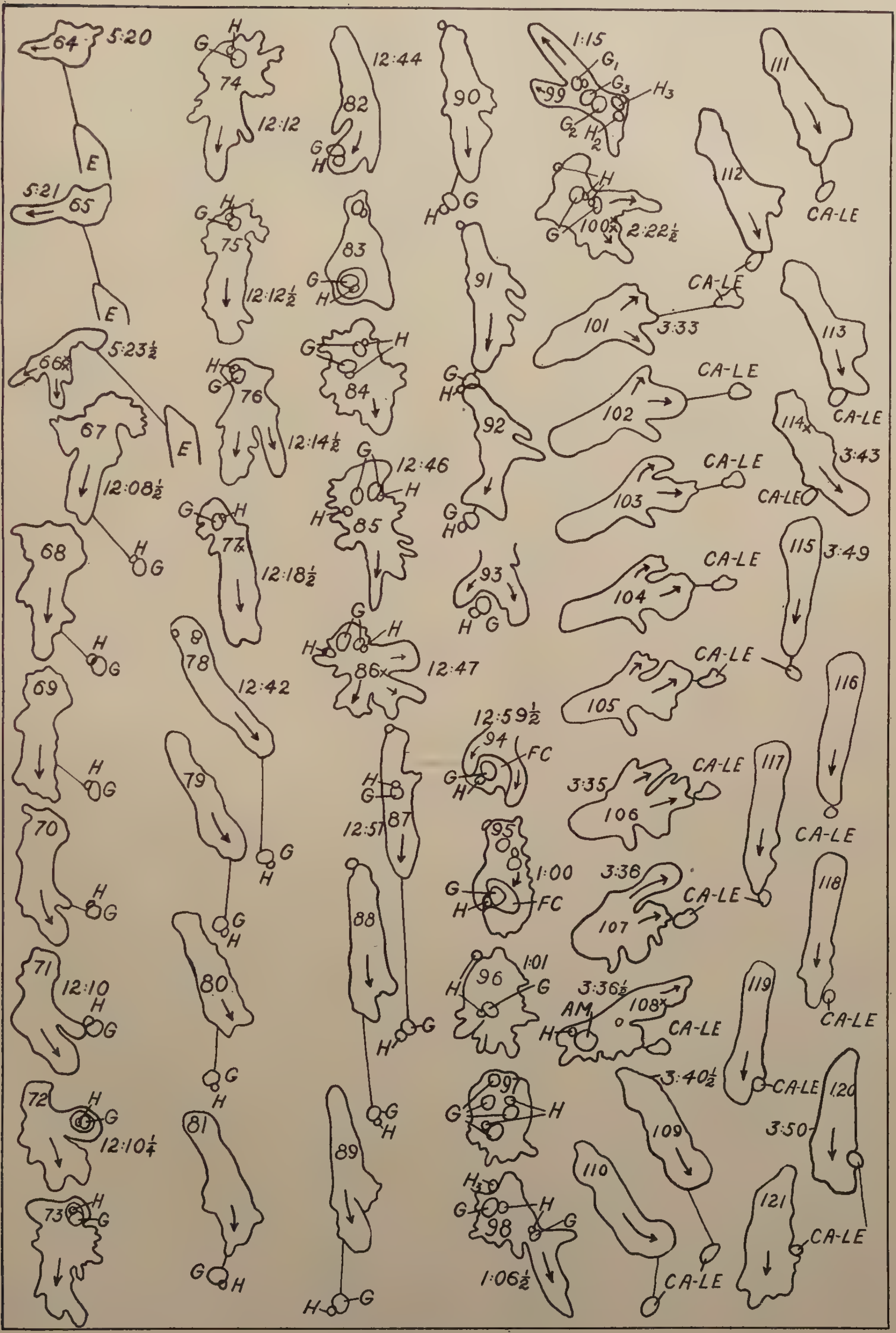
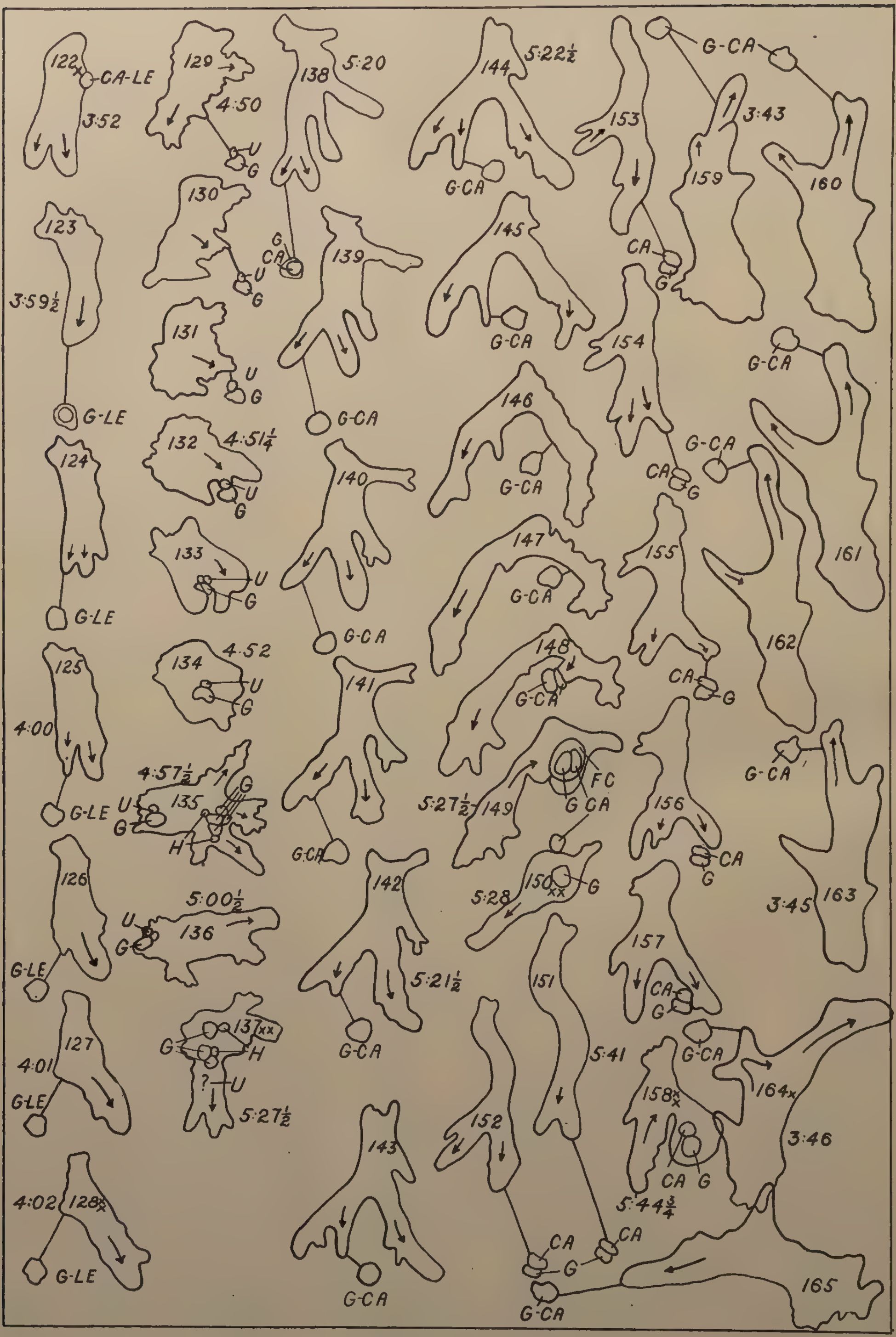
5:07
5:11½
E
S
G

Figures 1—63.

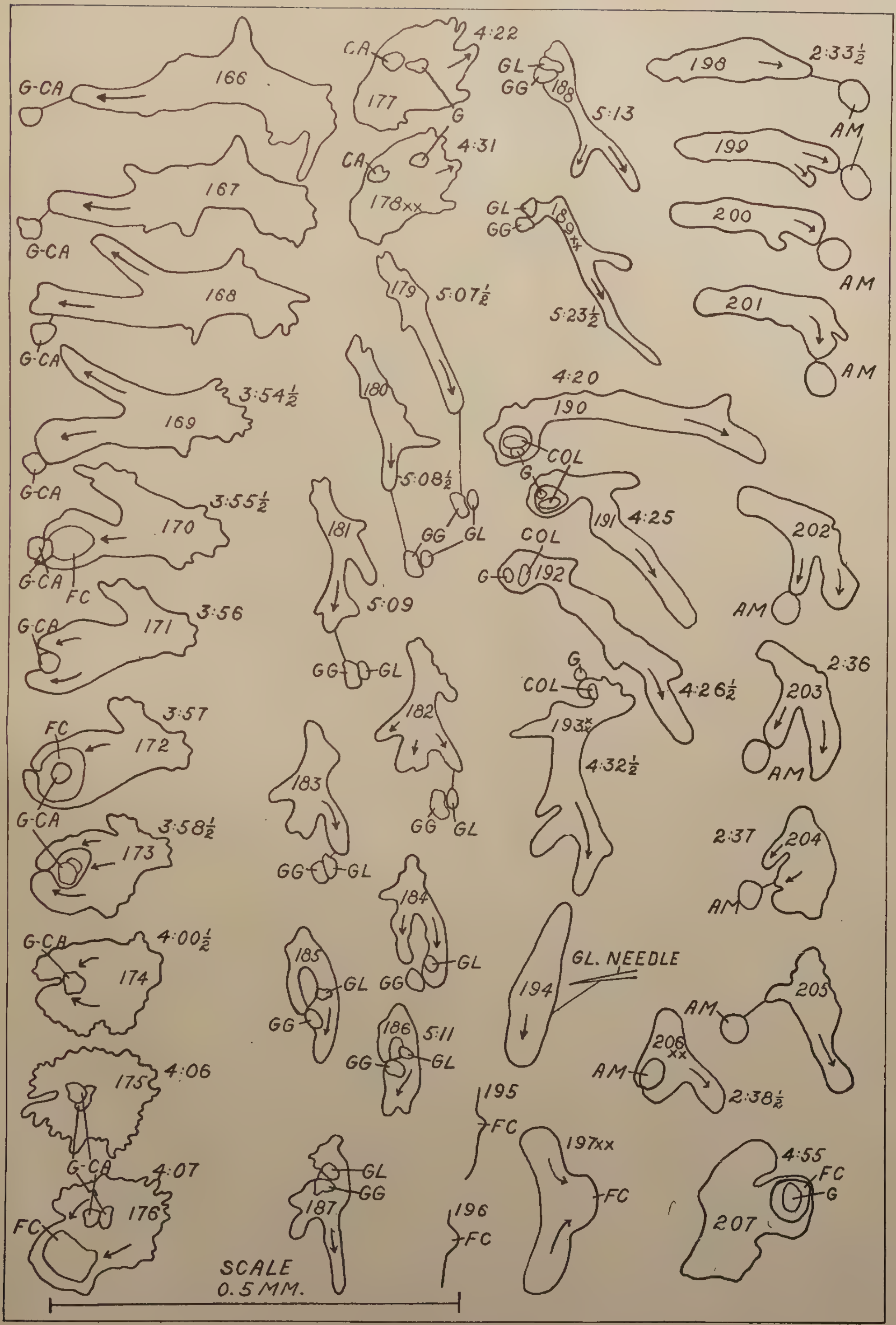


Figures 64—121.

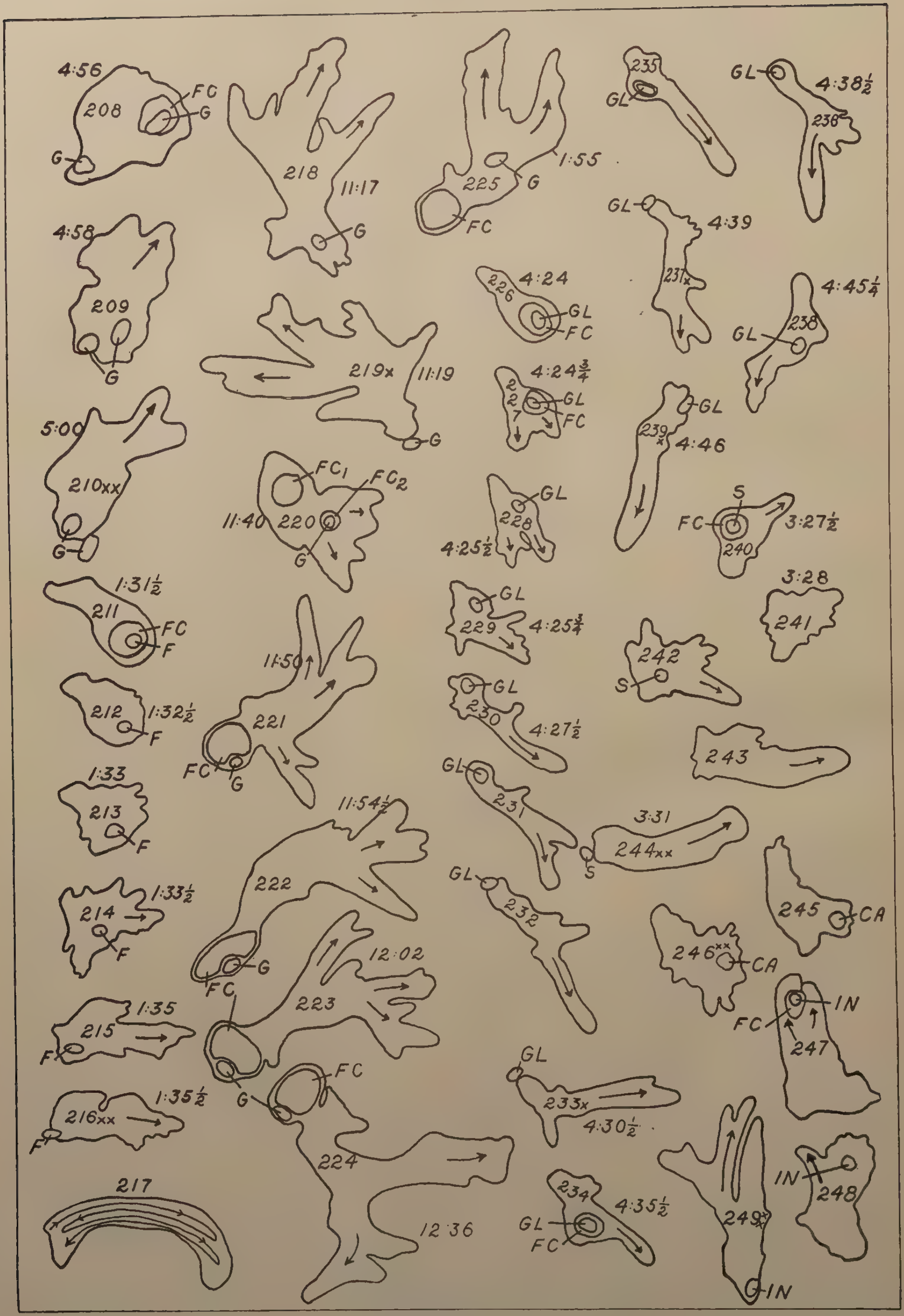
PLATE 3



Figures 122—165.



Figures 166—207.



Figures 208—249.

MAZE STUDIES WITH THE WHITE RAT

I. Normal Animals

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INTRODUCTION

The work of Watson, Bogardus and Henke, Vincent, et. al. has shown that the white rat learns the standard type of maze primarily in tactual and kinaesthetic terms, that during the learning the control is gradually transferred from contact to kinaesthesis, and that after the problem is thoroughly mastered the act is to be regarded as a kinaesthetic-motor coordination with an occasional reliance upon contact in times of emergency.

The neglect of the senses of vision, audition, and smell in the process of acquisition is not due to any functional incapacity of these senses. Miss Vincent has demonstrated quite conclusively that with a proper arrangement of the mazes both vision and smell will be effectively utilized in the development of the maze habit. Neither can it be affirmed that no optical, auditory, or olfactory data are present in the standard maze situation; rather we must conclude that for the rat organization these data as compared with those of contact and kinaesthesis are inadequate for the solution of this particular kind of a problem. The maze habit can be regarded as a definite sensorimotor coordination which was developed and which functions within a larger sensory environment. Many of these environing sensory conditions remain relatively constant and stable during the mastery of the maze.

Our experiments were designed to test the dependence of the maze coordination upon the stability of the wider sensory environment in which it was developed. The method consists of varying these environmental conditions while the maze is being learned or after it is mastered. In the usual type of experiment the rats are transferred from the living cage (kept in a constant position) to the maze located in a different environment. It is thus possible to alter the sensory conditions of the animal while running the maze, or to effect changes in the environment prior to the test.

Various maze patterns were employed in the experiments. Unless otherwise stated, the mazes were of the usual type with the exception that they were almost water tight and covered by closely fitting glass covers. These features are mentioned because presumably they may effect the sensory relation of the animal to the extraneous environment. In order to alter the objective environment of the maze, recourse was had to a canvas top. A light but rigid frame was constructed and placed upon the maze. Over this was stretched several thicknesses of canvas fastened at the top but hanging loose on the four sides. From the top was suspended an electric lamp. The interior could thus be illumined or darkened, any of the four side curtains could be raised or lowered, or the whole top could be removed or replaced at will.

This paper describes the experimental results on animals with intact sense organs. Nearly two hundred rats were utilized in the various tests. Some of the results were secured by students working under my direction. The majority of the tests were performed by the writer.

The disturbances induced by the alterations were measured in terms of the error record. These records embrace such features as the number of animals affected, the number of trials in which error was present, the number of errors, the length of time necessary to adapt to the novel situation, and the tendency for the disturbing effect to be carried over to subsequent tests under normal conditions.

EXPERIMENTAL RESULTS

A. Alteration of conditions previous to running the maze.

Variable Route. In the typical experiment the living cage is kept on a rack some distance from the maze and the animals are carried by hand and placed within the maze. This route was kept constant while the maze was being mastered. After mastery this route was altered in various ways. Sometimes a long and devious route through the laboratory was chosen. Fourteen rats were tested and no disturbing effects were noted.

Method of Handling. The normal method of handling was varied by inducing a condition of dizziness just before placing the animals in the maze. The rats were held at arm's length and whirled rapidly around in horizontal and vertical circles and then placed in the maze. The dizziness effects were evident in the animal's behavior. They experienced difficulty in standing erect, crouched down on the floor of the maze, and waited for the effects to disappear before attempting to run. Twelve animals were employed and no disturbances were present.

Position of Cage. After the maze was learned, the living cage was transported to a new position in the laboratory, care being taken to preserve its original cardinal orientation. This alteration introduces two new features, a new route to the cage, and a new sensory environment previous to the maze reaction. Since variations in the route are without effect, this aspect of the alteration may be neglected. The duration of the exposure to the novel environment prior to the test was varied; the animals were tested either 15 minutes or 24 hours after the alteration. The distance over which the cage was moved also varied. Ten animals were tested. Seventy per cent of these were affected, and the disturbance was present in but 41 per cent of their trials. The degree of disturbance varied with the degree of alteration. One group of six rats was subjected to alternating small and large shifts in the position of the cage and the resulting average error records were .58 and 1.75 respectively. The animals quickly adapt themselves to these changes. Most of the disturbances resulted from the 15 minute exposures and in this case the disturbing effect had generally disappeared on the subsequent day's test. There was no evidence that the effects persisted for any length of time after a return to normal conditions.

Covering Cage. After the maze was mastered, the living cage was entirely covered with several thicknesses of canvas. This substituted a homogeneous for a heterogeneous visual environment and reduced the illumination of the cage very appreciably. The animals were kept in this environment for a day before the first test. Forty-five animals were subjected to the experiment. But one rat exhibited signs of disturbance and the effect was present only in the first day's test.

Rotation of Cage. The living cage was rotated in reference to the cardinal positions while remaining in the same position.

The shifts employed were 90, 180, 270 degrees. The duration of exposure to the novel conditions prior to the test was varied. Three groups of animals were utilized and the conditions differed so that a separate description for each group is necessary.

1. The first group consisted of six rats and both living cage and the maze were uncovered. The rats were first subjected to the new orientation for 15 minutes and then tested in the maze. The cage was then returned to its normal orientation and control tests were given on the second day. On the third day the animals were tested for the effects of a 15 minute exposure to a different orientation. No animal was disturbed by these 15 minute exposures. Exposures of 24 hours were given for three orientations on successive days. All of the rats were disturbed by these alterations. The average error record per trial for six tests was 2.86. Errors were present, however, in but 40 per cent of the trials. There was a marked individual difference in susceptibility, the number of errors ranging from 3 to 44. The degree of the disturbance increased with successive shifts, though the rats quickly adapted themselves when kept in a given orientation.

2. The cage was covered with the canvas top and then rotated. The animals were tested in an uncovered maze. The group consisted of forty-five rats. They were tested immediately after the rotation and then for several days in succession. Three successive shifts were made before the cage was returned to its normal orientation. But seven of the rats manifested signs of disturbance and the effect was slight and quickly eliminated. With one animal the effects were sufficiently obvious that a disturbance can hardly be doubted. The effect was present for the first day's test for two positions.

3. In this experiment the uncovered cage was rotated, and the animals were tested in a covered maze. The animals were subjected to one or more day's exposure to each new orientation before being tested. Seventeen animals were employed, and signs of disturbance were noted for but five. The effect was so slight in four cases that one cannot be confident of the results. The disturbing effect was obvious for one rat for two of the new positions.

B. Alteration of conditions while running the maze

Degree of Hunger. After the maze was mastered, periods of four days of heavy feeding were alternated with similar periods of normal feeding. We thus have the rats coming to the maze with different degrees of hunger, the object of the test being to determine the effect of strength of motive upon the accuracy of a well automatized act. Rats differ very materially in the length of the feeding period necessary to keep in good condition and to give consistent daily records. These individual differences are due to the rate of eating and the amount of food required. The normal time allowed for eating ranged from 5 to 7 minutes. The periods of heavy feeding were 15 to 20 minutes in length, the animals being allowed to gorge themselves to their utmost capacity. Ten rats were tested. Heavy feeding multiplied the average error record by twenty. All rats were affected in varying degrees. Disturbance was present in but one-third of the trials. The degree of the disturbance was highly irregular from trial to trial. In general the effect increased at first and then decreased. Complete adaptation was never secured.

Cleansing Maze. During the course of a long experiment, the maze will accumulate considerable filth in spite of the glass cover. This filth consists of faeces, wisps of cotton, shells of sunflower seeds, trackings of milk, and urine deposits. These were allowed to accumulate for considerable time and the maze was thoroughly cleansed and washed. The animals were tested on subsequent days to determine the effect of this alteration of conditions upon the accuracy of the maze habit. Ten rats were tested, and eight were affected. The greatest effect occurred on the second trial. Adaptation was secured in four trials. Errors were present in but 60 per cent of the tests. The average error record per trial for those affected was 1.75.

Covering Maze. The rats were allowed to master the uncovered maze. The canvas top described in the introductory section was then placed over the maze. In one case the interior of the top was illuminated when the rats were tested, and with another group it was not. A homogeneous maze environment was thus substituted for the customary heterogeneous one, and the illumination was either decreased or altered in character. Eighteen rats were subjected to these changes while running the maze, and none were disturbed in the slightest degree. This fact would indicate that the rat does not rely upon stimuli from the extraneous environment during the later stages of the learning process.

Uncovering Maze. The animals first mastered the maze while it was covered with the canvas top. After mastery this top was removed and the animals tested. Two slightly different experiments were performed. 1. The maze was mastered when the top was open on one side allowing poor daylight illumination of the interior. The top was now removed. Seven rats were tested and none were disturbed by the changes. 2. The maze was mastered while entirely closed and the interior illumined by an electric light. The top was now removed. There resulted the substitution of a heterogeneous for a uniform optical environment, and the introduction of daylight for artificial illumination. Ten rats were tested, and five were disturbed. The effects persisted from 1 to 6 trials. The errors were distributed irregularly, and perfect records were secured in 70 per cent of the tests. The average error record for those affected was 1.07 as compared with a previous normal of .20. The total number of errors per animal varied from 3 to 11.

Increase of Illumination. The maze was learned while entirely covered with the canvas top but without interior illumination. The interior was now illumined by the electric light. A well lighted uniform environment was thus substituted for a subdued one. Ten rats were tested, and seven were affected. The disturbance lasted from 1 to 6 trials. Errors were present in but 40 per cent of the tests. The average error record was 1.35 as compared with the previous record of .51. The total number of errors per individual varied from 4 to 47.

Decrease of Illumination. An open maze was mastered. It was situated in front of an open window giving a good illumination. After the maze was learned this window was covered so that practically all light from this source was excluded. This procedure decreased the illumination in the maze and altered its direction, without changing the character of the environing objects. Ten rats were tested and seven were disturbed. The effects lasted for 1 to 8 trials. The maximum effect occurred on the second test. Many trials were without error. The average error record was 3.18 as compared with a previous normal of .21. One animal made 40 errors in eight trials. After adaptation to the new conditions, a return to the normal situation effected no disturbance.

Position of the Experimenter. The experimenter maintained a constant position in reference to the maze while it was being learned. After mastery, this position was varied. After inserting the rats in the maze, the experimenter occupied a position on the opposite side of the maze from that in which he formerly had stood. Six rats were tested on successive days until all disturbance had subsided. All members of the group were affected in varying degree. Errors were present in 60 per cent of the tests. The average error record for three successive trials was 2.50 as compared with a previous normal of .11. The disturbance was eliminated in three trials. The total number of errors per rat for the three trials ranged from 2 to 18. The disturbance occurred only at that point in the maze path near which the experimenter stood. The path previous to and after this critical point was traversed normally. All error deviations were in the direction of the experimenter. A disturbance was frequently manifested by slow and hesitant movements and head and body orientations in the direction of the experimenter even when no errors were made.

Rotation of a Uniform Environment. The maze was covered by the canvas top closed on all sides and the interior was illuminated by the electric light. Under these conditions vision of the objective environment was impossible to the human eye. This top was practically square (3′, 9″ by 4′), and as a consequence the optical environment was uniform. The top was now rotated 90 degrees between trials, the maze itself remaining stationary. Presumably the visual situation was not altered by this procedure. Ten rats were tested, and no disturbance resulted.

Rotation of Heterogeneous Environment. The maze was learned with the curtain of the canvas top open on one side. This curtain was now closed and that on another side was opened. This procedure was continued until all four sides were opened several times on successive days. The alteration produced a change in the direction and intensity of the light as well as in the character of the optical environment. Seven rats were tested under these conditions, and five were affected by the novel conditions. These five animals made an average error record of 1.90 for six tests, and errors were present in 85 per cent of the trials. The disturbance due to the alteration persisted to some extent on the subsequent day's test in normal conditions. The number of errors per rat ranged from 9 to 15. A repetition of the test for each of the three novel situations exhibited a pronounced tendency toward adaptation, but the experiment was not continued until complete adaptation was secured.

Position of the Maze. After being learned, the maze was removed to a new position in the laboratory but its original cardinal orientation was preserved. The maze was shifted about twelve feet in position but the shift was of such a character that the maze was now situated in practically a new environment. This procedure involved two alterations; a change in the objective environment while running the maze, and a new route from the living cage to the maze. The latter factor has been shown to be non-effective and may thus be disregarded. Six rats were given three tests in the new position, and four were affected. These made errors in 55 per cent of the trials, and gave an average error record of 2.08. The number of errors per rat ranged from 4 to 10. The animals adapted quickly to the novel conditions, and in some cases a slight disturbance was evident on a return to the old position.

Rotation of Maze. In this experiment the canvas top was not used, and as a consequence the maze was rotated in reference to a stationary heterogeneous environment. This experiment was first performed by Professor Watson and our results are in harmony with those secured by him. Unless otherwise specified, the three novel positions utilized were 90, 180, and 270 degrees. The tests were conducted on different mazes and with different procedures and thus need to be described separately.

1. The glass covered maze was used and tests were given for the three novel positions on successive days followed by a return to the original position on the fourth day. This procedure was now repeated to determine the effect of adaptation. Ten rats were employed and all were disturbed. In the first shift, errors were present in 65 per cent of the trials, and an average error record of 6.95 was secured. The induced effect was occasionally carried over to the subsequent day's trial in the normal position. A repetition of the shifts disclosed a pronounced adaptive tendency. All members of the group were

still affected but the percentage of perfect trials was increased from 35 to 53 and the error record was reduced from 6.95 to 1.72. The shifts were not continued until complete adaptation was effected.

2. The same conditions obtained in this experiment except that the maze was left in each new position until the disturbance was eliminated. After adapting to the three positions, the maze was returned to the normal position. This procedure was now repeated until complete adaptation was effected for the four rotary positions. Similar rotary shifts were now instituted between the 45, 135, 225, and 315 degree positions until adaptation for these positions was effected. Fifteen animals were employed in the experiment. During the first rotation, thirteen animals were disturbed, and these gave an average error record of 10.7 for the first day for the three new situations. The rats were not affected in every trial, as perfect records were secured in 32 per cent of the first day's trials. Adaptation was effected for each position on an average of four trials. The induced disturbance was occasionally carried over to a slight extent to the normal position of the maze. The adaptation for each position secured in the first shift was not permanent. New rotations disclosed a further disturbance, but the effect gradually decreased with repeated shifts; fewer animals were disturbed, the errors became smaller, the percentage of perfect trials increased, there was less carrying over to the normal position, and the time necessary to adapt for each position was lessened. Complete adaptation was effected on the fifth repetition and thereafter the maze could be rotated at will between any of these four positions without disturbance. Complete adaptation for one series of positions does not, however, involve adaptation to another series of positions. Rotary shifts were now instituted between the 45, 135, 225, and 315 degree positions. In the first shift all of the rats were again disturbed. In the first day's trials for the four positions, the average error record was 7.2 with a percentage of perfect runs of 20. Adaptation was again effected with repeated tests.

3. A group of animals was rotated in a well illuminated and a darkened environment. The maze had been learned with the illuminated condition. The room was darkened by means of window shades. The animals were accustomed to running the

maze under both conditions before the rotation tests were given. One set of four rats were tested for three positions on successive days when the room was well illuminated. The tests were now repeated for the darkened environment and these were followed by a series with an illuminated maze. The average error records for the three conditions respectively were 7.15, 1.90, and 3.20. The final value for the illuminated environment is thus greater than that previously secured for the darkened condition in spite of the fact that animals tend to adapt to these rotary shifts when repeated. With a second set of six animals, complete adaptation was effected for three positions while the room was darkened. The room was then illuminated, and the tests were repeated. A disturbance was again evident. The disturbance could hardly be due to the sudden introduction of the light, as the maze had been learned under these conditions, and the rats had been accustomed to run the maze in its normal position while the room was illuminated. The results indicate that a maze rotation in reference to a well illuminated environment is more disturbing than a similar one in reference to a darkened environment.

4. A sideless maze was employed in the following experiment. This consists of a series of runways separated from each other by open spaces four inches in width. This maze differs from the standard maze usually employed in these experiments in several respects:—it is less complex as to number and length of alleys, the absence of sides eliminates the possibility of a contact guidance in traversing the paths, and the absence of the sides and the glass cover allows the animals a more intimate sensory contact with the objective environment. We were interested in comparing the degree of disturbance due to rotation on such a maze with that exhibited by animals in the standard maze. If rotation disturbs the animals because of the alteration in reference to the environment, the degree of disturbance in the sideless maze should be the greater. Five rats were tested. The average error record, and the number of trials necessary to secure adaptation were twice those for the standard maze. This ratio does not adequately represent, however, the relative confusion in the two cases because it neglects the greater simplicity of the sideless maze. If the two mazes offered equal opportunity for error, it is safe to assume that the discrepancy

between the two sets of values would have been much greater than they were. This difference in complexity can be equated by comparing the initial error record due to rotation with the initial error record in learning. The average error record for the first trial in learning the standard maze was 44, while the average number of errors made in the first rotation test was 10. Rotation in the standard maze produces an initial error disturbance which is approximately 23 per cent of that in mastering the maze. The initial error record for the sideless maze was 10.5, while the corresponding value for rotation was 19.7 The confusion involved in rotation was thus greater than that in learning. Relative to the number of initial errors in learning, rotation in the sideless maze produces a disturbance eight times as great as in the standard maze.

Certain peculiarities of behavior were apparent in the sideless maze. The rats frequently gravitated to that corner at which the food box had been located before the rotation. Failing to find food, they renewed their explorations of the maze, but came back again and again to this particular corner. One animal finally refused to leave this locality and had to be removed from the maze. After two such unsuccessful trials on successive days, the experimenter guided the animal to the new position of the food box, and thereafter the maze was traversed successfully on the animal's own initiative. One other rat was unsuccessful on the third trial. This type of behavior was exhibited in varying degrees during the first three trials by each of the ten rats employed in the test. Such behavior has been observed but rarely in a standard maze and only when certain parts of the maze were flooded by strong daylight illumination.

5. The *cul de sacs* in the standard maze were closed by sliding doors. After learning the maze in this condition, the animals were subjected to the usual rotation tests. Obviously all disturbance due to rotation must be measured by return errors. Twelve rats were tested and all were affected. The experiment is significant in indicating that the disturbance in maze rotation is not due exclusively to wrong choices at those critical positions from which several paths diverge. Confusion obtains when no choice is possible and when the animals have had no experience with *cul de sacs* during learning.

Rotation of Maze and Environment. The maze was learned while entirely covered by the canvas top and illuminated by an electric light. After learning, both maze and top were rotated as a unit. Tests were given for the three positions on successive days. On the fourth day a normal record was secured for the original position. The above procedure was then repeated several times. Ten rats were utilized in the experiment. In the first shift eight rats were disturbed; these gave an average error record of 1.29 for 48 trials, although errors were present in but 31 per cent of the trials. The shifts were now repeated three times and no tendency toward adaptation was in evidence. The percentages of animals affected in the four successive shifts were 80, 80, 90 and 70. The percentages of trials in which error was present were 31, 35, 55, and 36. The error records were 1.29, 1.81, 1.18, and 1.32. The largest disturbance occurred for the 180 degree position. This result is a function of the position and not of the temporal order of the shifts, inasmuch as a different temporal order of the three positions was given in the successive series.

This experiment is comparable with the first test of the previous section in all respects except the environmental conditions. In the previous test the maze was rotated in reference to the environment, while here both maze and environment were rotated. Rotation in reference to a stationary environment produced much the greater effect at first, and allowed a pronounced degree of adaptation when the experiment was repeated. No adaptation was present when both maze and environment were rotated, and the records secured were practically identical with those in the former experiment after the rats had become adapted.

C. Alteration of conditions while learning the maze

Rotation of Maze. Animals were required to master the standard maze when its cardinal orientation was changed for each day's test. The daily shifts in position were 90 degrees, each position being repeated every fourth day. These records are compared with those representing the mastery of a stationary maze, and we are able to estimate the relative effect upon learning of a stable vs. a variable relation to the objective environment. The following records for a rotated maze were obtained from ten rats without previous laboratory experience:—the average number of trials involved in mastering the maze was 30, a group error record of zero was first obtained on the 36th trial, and the average number of errors made during learning was 196. The corresponding values for a group of 29 rats learning the same maze while stationary were 18, 22, and 144 respectively. Rotation thus increased these values by 50 per cent. A comparison is likewise possible between two groups of rats which had had previous experience upon a different type of problem. Ten rats in learning a rotated maze mastered it in 21.4 trials, first secured a perfect group record on the 27th trial and averaged 110 errors per rat for the learning period. The corresponding values for 14 rats in mastering the same maze while stationary were 9.2, 17, and 58. In this case rotation has doubled the difficulty of learning. The two curves of learning were similar in form; rotation seems to add on the average about 3 or 4 errors to each trial and this slight addition towards the end operates to postpone the final mastery of the maze for many trials.

Uniform Environment. Certain groups of rats mastered the maze when covered on all sides by the canvas top. Other groups also mastered this maze without the top. In one case the maze habit was developed in a uniform optical environment, and in the other with a heterogeneous environment. A comparison of the two sets of data will thus indicate the function of a heterogeneous environment in the development of a habit. The heterogeneous environment aided learning. The average number of trials and the average number of errors per rat for a group of 29 rats in mastering an open maze were 18 and 144 respectively. The corresponding values for the closed maze were 26 and 282. These results indicate that the animals may utilize data from the objective environment in mastering the maze.

CONCLUSIONS

Any sensori-motor act can not be regarded as an isolated independent function; the act was learned within a wider sensory environment, and it never ceases to be wholly free from these conditions either during or after its development. The stability of the environment furthers the development of the act, and conditions the regularity and accuracy of its functioning after it has become automatic. These environmental conditions embrace the sensory situation at the time, the sensory situation in which the animal lived for several days prior to the act, as well as the intraorganic condition of the animal. The influence of intraorganic factors is evident from four types of facts:—1. The case of hunger is obvious. 2. Novel situations while running the maze may induce effects which persist and exert a disturbing influence after a return to normal conditions. These persistent disturbing effects must be intraorganic. 3. Alterations of the cage environment previous to the performance of the act may exert a disturbing effect. Evidently these disturbing conditions must be retained as some intraorganic condition. 4. The influence of some of these alterations may be cumulative from day to day.

These alterations operate in an irregular and sporadic fashion. This generalization is supported by several lines of evidence. 1. A few animals in each group are usually immune to the altered conditions. In the majority of experiments the percentage of animals affected ranged from 50 to 90. 2. Animals may be disturbed in one trial but immune in another. The percentage of trials in which error was present ranges from 30 to 65 for the various experiments. On the average the affected animals were not susceptible to the alterations in one-half the tests. 3. An animal may be susceptible to one kind of alteration but immune to another, while the opposite relation will obtain for another rat. Eleven rats were subjected to the following five experiments,—position of experimenter, rotation of cage, position of cage, position of maze, and rotation of maze. Three animals were disturbed in all five experiments, three rats were affected in but four tests, two rats in three tests, two rats in two experiments, and one rat in but a single test. Two rats were disturbed by the rotation of the maze, but were not affected by a change in the position of the maze; on the other hand, two rats were disturbed by the latter test but were immune to the rotation of the maze. Ten rats were given the following tests, increase of illumination, rotation of maze and environment, cleansing paths, uncovering maze, and rotation of maze. One rat was affected by all tests, three rats were immune to one experiment, four to two experiments, and two to three experiments. Three animals were immune to the rotation of the maze and environment, but were disturbed by cleansing the maze; on the other hand two rats were immune to the changes involved in the cleansing of the maze but susceptible to the first experiment. Many similar illustrations can be given. 4. A rat may make a very large number of errors in some tests and very few errors in others. Ten rats were ranked as to the number of errors made in each of five experiments. The rankings given to one rat for the five experiments were 1, 2, 9, 2, and 2. Similar rankings for another animal were 8, 1, 1, 7, and 9. This lack of consistency may be shown by dividing the animals into two groups on the basis of number of errors. Only one of the ten rats belonged to the better half in all five experiments. In another group of eleven rats but four manifested any high degree of consistency; two were found in the better half for all experiments, while two invariably belonged to the poorer half. The rankings for one experiment were correlated with those for the other four experiments, and positive values of .369, .690, .414, and .068 were obtained. 5. Affected animals make a relatively high percentage of perfect runs in one experiment and a low percentage in another. 6. One would naturally expect a high degree of correlation between the total number of errors made in an experiment and the number of trials in which a disturbance was present. Two groups of animals were ranked in both respects for five experiments and the correlation values were computed. Small negative values were obtained in every case. These results mean that those animals which make an extremely large number of errors in one trial are likely to become adapted to the alteration and run the subsequent trials without error. 7. Animals that do well for one position in the experiment on maze rotation do not necessarily make good records for other positions. The correlation value between two positions for a group of nine rats was but .434. Animals that do well for one position do not necessarily make good records when the test for this position is repeated. Such a correlation by the ranking method for the above group of rats gave a value of but .024.

The above emphasis upon the irregular and accidental character of the disturbances must not blind one to the fact that some rats manifest a relatively high degree of consistency in the various experiments. Some animals are quite susceptible and make a large number of errors in every experiment. Other rats are prone to immunity; they either fail to be disturbed or make low error scores in every experiment. This consistency is limited to comparatively few animals; irregularity and inconsistency obtain for the majority of the rats and for the groups taken as a whole.

Adaptability to these alterations is the general rule. The rate of adaptability is a function in general of the magnitude of the disturbance. Stability of the novel conditions aids adaptation, while any further change delays it; animals kept in a novel situation eliminate the disturbance more quickly than when they are shifted back and forth between the novel and the normal conditions. Continuous alterations of the novel conditions as in the various rotation experiments operate to delay the adaptation. Adaptation to any novel situation is in the main specific and not general; the animals become adapted to that particular alteration and not to all novel situations. There is no conclusive evidence that the adaptation secured in one experiment operates to give complete immunity in other experiments. Complete adaptation to one series of positions in the rotation experiment did not involve a complete immunity for alterations between another series of positions. Any adaptation to a particular situation is retained with some degree of perfection over a period of time devoted to securing adjustments to other novel conditions. Any acquired immunity is thus mainly specific and refers only to that situation under which it was acquired; it is retained after the interpolation of other tests with some degree of perfection, but it gives no certain aid to the mastery of other novel situations.

The degree of disturbance was a function of the kind of alteration. As a general rule alterations while running the maze were more effective than changed conditions of the rat's environment before being placed in the maze. It is rather surprising that pronounced changes in method of handling and of route from cage to maze should be without effect, while alterations of the living cage in relation to its environment were provocative of error. The difference in the results may be due to the fact that the animals were not subjected to a sufficient duration of exposure to the novel conditions in the former two experiments. The maximum duration of exposure never exceeded a few minutes, while the minimum exposure in the cage experiments was fifteen minutes. Covering the maze produced no effect, while considerable disturbance was manifest when the maze was uncovered. This difference in results is more comprehensible when the situation is stated in the following terms:—The removal of stimuli (change from a heterogeneous to a uniform environment) is without effect, while the introduction of novel stimuli operates as a disturbance. This conception would indicate that the rats after mastering the maze do not rely to any great extent upon the objective stimuli as guides or controls in traversing the maze, and that the introduction of unfamiliar conditions operates as a distraction.

This paper makes no pretense of defining in physical terms the nature of the environmental alterations. Rotation of the maze may disturb the normal relation of the animal to the optical, olfactory, or auditory aspects of the environment. Likewise we make no pretense of knowing through what sense avenue these disturbances were mediated. We were interested primarily in establishing the fact that the rats are sensitive to these alterations in some way and that stability of sensory conditions is conducive to the development of an automatic act.